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TORSIONS INDUCED BY AUXIN

By R. SNOW

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(With 1 figure in the text)

It was reported in a previous paper of this series (1945, p. 77) that petioles of various species and plagiotropic stems of *Philadelphus*, if given a streak of hetero-auxin in lanoline applied on one side, twist so as to raise the treated side up to or towards the top. It was also shown by an experiment on petioles of *Phaseolus multiflorus* that the rule is that the torsion raises the treated side towards the top: for it did so even when the whole plant was inverted, although the direction of torsion was then the opposite in relation to the structure of the petiole. It was concluded that the treated side comes to act physiologically in relation to gravity like a dorsum; and it was further thought probable that the *normal* geostrophism of such lateral members, which brings the morphological dorsum to the top, is related to a tendency to accumulate the natural auxin in higher concentration along the dorsum.

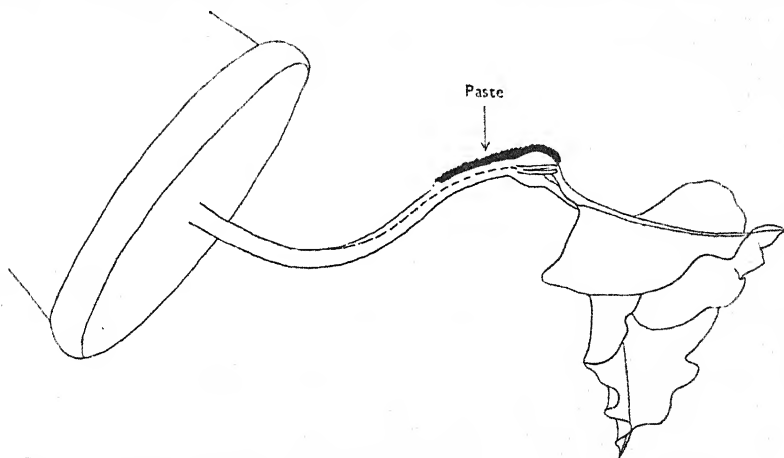


Fig. 1. *Phaseolus* looked at horizontally after 54 hr. The dotted line was on top at the start, and the paste was on the far side.

These results suggested the question whether *orthotropic* stems, roots and coleoptiles would react in a similar way if laid horizontal and treated with hetero-auxin in lanoline on one side; and accordingly the following experiments were carried out. Four seedlings of *Phaseolus multiflorus* were grown in pots, and when the epicotyls were elongating rapidly, the paired first leaves being 5 or 6 cm. long, the pots were laid on their sides in overhead light so that the epicotyls were horizontal with the plane of the leaves also horizontal. Then a thin streak of lanoline containing hetero-auxin at a concentration of 1 in 275 was placed along one side of the distal 1.2 cm. of the epicotyl and was continued for a little way along the ventral face of the petiole of the leaf on that side. The four epicotyls all twisted in such a direction so as to raise the paste from the lateral position towards the

top, the torsions being after $6\frac{1}{2}$ hr. roughly 75° , 60° , 30° and 30° , and after 23 hr. 80° , 60° , 60° and 50° . The figure shows the third of these seedlings drawn as seen horizontally after 54 hr., when it had twisted 80° .

Four seedlings of *Pisum sativum* were similarly placed horizontal, with the plane of the leaves horizontal, and in each of them a young internode, only about 2 cm. long, was given a thin streak of the same paste along its distal half on one side. The paste was continued apically for a little way along the petiole on that side. In all four seedlings the treated internodes twisted so as to raise the paste, the torsions being after $6\frac{1}{2}$ hr. 90° , 80° , 80° and 70° , and after 23 hr. 90° , 90° , 90° and 80° .

Two young sunflower seedlings, with hypocotyls 5 and 2.5 cm. long, were placed horizontal with the plane of the cotyledons horizontal, and a very thin streak of a hetero-auxin paste of 1 in 400 was placed along the distal 1 cm. of each hypocotyl on one side and for a little way along the petiole of the cotyledon on that side. The hypocotyls twisted so as to raise the paste, the torsions being 90° and 70° after 23 hr.

Three young tomato seedlings, with hypocotyls only 2 cm. long, were treated like the sunflower seedlings, but with the paste of 1 in 275. The hypocotyls all twisted so as to raise the paste, the torsions being after 30 hr. 50° , 35° and 15° , and after 54 hr. 50° , 50° and 25° .

Six oat seedlings grown in the dark were placed so that the elongating coleoptiles were horizontal with their longer transverse diameters horizontal, and each was given a streak of this 1 in 400 paste along one side. The coleoptiles all twisted so as to raise the paste, the torsions being after 23 hr. at about 17.5° C., 110° , 90° , 90° , 90° and 90° .

Eight young seedlings of *Vicia faba*, with main roots still quite short, were each given a streak of a hetero-auxin paste of concentration only 1 in 6000 on one of the narrow sides of the root. The paste reached from the level of the apical meristem to about 5 mm. behind it. The seedlings were then replaced in loose damp sawdust so that the roots were horizontal with their two narrow sides horizontal. Little shields prevented the sawdust from falling on to the treated apical parts of the roots. The roots all twisted so as to raise the paste, the torsions being after 23 hr. 70° , 65° , 50° , 45° , 40° , 40° , 30° and 25° .

Thus all the organs tested twisted so as to raise the sides treated with hetero-auxin paste.

Naturally the various organs made curves as well as torsions, the curves of the stems and coleoptiles being at first curves away from the paste in the horizontal plane and geonegative curves in the vertical plane. In the four *Phaseolus* epicotyls, for example, at $6\frac{1}{2}$ hr. the horizontal curves were 60° , 50° , 40° and 20° , and the vertical curves 45° , 25° , 20° and 30° . But by this time they had made torsions raising the paste which ranged from 30° to 75° , so that from this time onwards the tendency to curve away from the paste was directed obliquely downwards and partially counteracted the negative geotropism. Consequently after this time the curves in the two planes did not increase much more, and some of them diminished. Similar results were noticed in the other species also.

The various orthotropic stems and coleoptiles which were placed horizontal and had one side treated with hetero-auxin paste were thereby made to curve as well as twist like plagiotropic stems; and this resemblance was not only in the final result, but in the process leading up to it. For it is now generally accepted that normal plagiotropic stems, and also leaves, commonly owe their orientation to a balance between negative geotropism and an opposing tendency which may be called epinastism. Correspondingly in the stems

and coleoptiles treated with auxin paste, the curvature away from the treated side, which became physiologically dorsal, opposed the geonegative curvature after the treated side had risen by torsion, just as does in natural plagiotropic stems the epinastic curvature away from the natural dorsum. But it remains to be discovered how it comes about that the face of a stem or petiole which is physiologically dorsal, either naturally or through being treated with hetero-auxin, tends to rise by torsion to the top.

The fact that the roots, though positively geotropic, twisted like the stems so as to raise their treated sides need not be surprising, since in roots as in stems auxin is diverted towards the lower side. In the roots the horizontal curvatures were rather strong, and were of course towards the paste.

Incidentally it was noticed that in the stems of *Phaseolus* and *Pisum* the torsions and the curves away from the paste were carried out by the auxinated zone of the stem itself and by a rather short zone just basal to it, whereas the geonegative curves were carried out by a zone further towards the base which was mainly or entirely separate. Consequently, after a day or more, when the stems had twisted so that the two curves were nearly in the same plane, the total curve was S-shaped, as is shown in the figure; and similar S curves were noticed in the coleoptiles.

It needs finally to be considered whether the torsions may have been caused by the two curvatures. This is made unlikely by the fact that in *Phaseolus* and *Pisum* the two curves, when present, were mainly in different zones. Moreover in two of the *Pisum* stems the geonegative curves at 6½ hr. were nil, and in the other two only 25° and 35°. But it seemed desirable to test directly whether in similar stems curvatures in two planes do cause torsions.

So seven similar *Phaseolus* seedlings were arranged with their epicotyls horizontal, and when these had curved up about 60° the pots were rotated through 90°, so as to stimulate them in the plane at right angles. When the components of the total curvatures in the new vertical plane were from 40° to 75° (mean 47°), it was found that the earlier curves, which were now the components in the horizontal plane, were still from 20° to 35° (mean 29°); but there were no torsions. With the same method two short young sunflower hypocotyls were stimulated in two planes at right angles, the component curves being in the one hypocotyl 45° and 80° simultaneously, and in the other 20° and 45°; but again there were no torsions.

So in young stems of *Phaseolus* and *Helianthus* similar to those used in the experiments with auxin paste, two curvatures induced in planes at right angles are not necessarily accompanied by a torsion, and it therefore seems that in the experiments with the paste the torsions cannot have been caused by the two curvatures.

The results of these last experiments are contrary to the statement of Staub (1934) that in many organs, including hypocotyls of *Helianthus*, a convex face acts as if physiologically dorsal. For if so the face which became convex in the earlier geotropic curvature should have risen by torsion when the pots were rotated through 90°. But it seemed possible that longer and weaker sunflower hypocotyls, such as would sag when placed horizontal, might twist when similarly stimulated in two planes. For Rawitscher (1932, p. 195) mentions that many long shoots, which are too weak to raise their own weight by geotropism when horizontal, make torsions. Actually it was found that two longer and weaker sunflower hypocotyls when similarly stimulated in two planes did make torsions of 30° and 70° such as to raise the convex side of the earlier curve. Whether any of the torsions

reported by Staub can have been caused in this way is not clear; but the torsions reported here, which were induced by hetero-auxin paste in organs that were not sagging, cannot anyhow have been so caused.

SUMMARY

1. Various young orthotropic stems, and also coleoptiles and main roots, when placed horizontal and treated on one side with hetero-auxin paste all twist so as to raise the treated side to the top, or towards it.
2. These torsions are not caused by the curvatures in two planes which are also induced.
3. The organs treated with the paste become plagiotropic, the treated side being physiologically dorsal.

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ON THE DETERMINATION OF LEAVES

BY MARY SNOW AND R. SNOW*

(With 10 figures in the text)

I. INTRODUCTION

We propose to present here and discuss evidence relevant to three suggestions concerning the determination of leaves which have lately attracted some attention. The first of these is that the bundle leading to a leaf (the leaf trace) is determined before the leaf itself and somehow determines the leaf. The second is that the superficial layer of the stem apex, the dermatogen, grows tangentially much more than the interior and so forms folds which become leaves. The third is that new leaves arise as far as possible from the existing young leaves, and that they do so because the existing leaves either consume growth-promoting substances or form growth-inhibiting substances. If these three suggestions are found untenable, we shall submit that it is time to consider seriously a theory of the determination of leaves, which we proposed previously, continuing the ideas of earlier workers, and supported with direct experimental evidence (1931, 1933, 1935).

2. THE SUGGESTION THAT LEAF TRACES DETERMINE LEAVES

The suggestion that leaf traces determine leaves is based on the claim that in some species the traces are formed before the leaves which they serve. Good evidence of this has been offered by Sterling (1945) for *Sequoia sempervirens*, and it is also claimed by Crafts (1943) for the same species. Gunckel & Wetmore (1946*a*, p. 294; 1946*b*, p. 539) consider that their observations show or suggest that in *Ginkgo biloba* a leaf trace starts to be formed before its leaf appears. Esau (1943, p. 254) thinks that the same is probable in *Linum perenne*. Priestley, Scott & Gillett (1935) concluded from an indirect argument that the same was true for *Alstroemeria aurantiaca*.

As to a determination of leaves by traces, Priestley *et al.* (1935) mentioned this as a possibility. Sterling (1945) considers that the traces may partially determine the leaves in *Sequoia*, but admits the serious difficulty that in his *Sequoia* apices variations in phyllotaxis did not all correspond with variations in arrangement of traces. Gunckel & Wetmore (1946*b*) are also inclined to support this suggestion for some species at least. Presumably the suggestion might be extended, with some loss of probability, to other species in which the traces are not formed before their leaves, if it were assumed that the presumptive path of a leaf trace is physiologically determined well before it becomes visible, and that it can then already determine in turn the position of its leaf.

This suggestion seems to us to conflict with the results of some of our previous experiments on *Lupinus albus* (1931, 1933); but, nevertheless, we thought it desirable to test it more simply and directly in young seedlings of that species by cutting transversely

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through the region just beneath the presumptive area of a young leaf due soon to arise, and seeing whether that leaf would then fail to arise or be much weakened or delayed.

In *L. albus* the phyllotaxis is spiral with contacts 1, 2 and 3, and mean divergence angle 136.30 ± 0.26 (Snow & Snow, 1931).* The contacts 2 and 3 are those most directly beneath each leaf, and are the most important, since the contact 1, with the next older leaf, is only just reached by the extreme edge of each of the youngest leaves. Transverse sections of a bud are shown in Fig. 1*a, b, c*. From each leaf three traces descend into the stem,

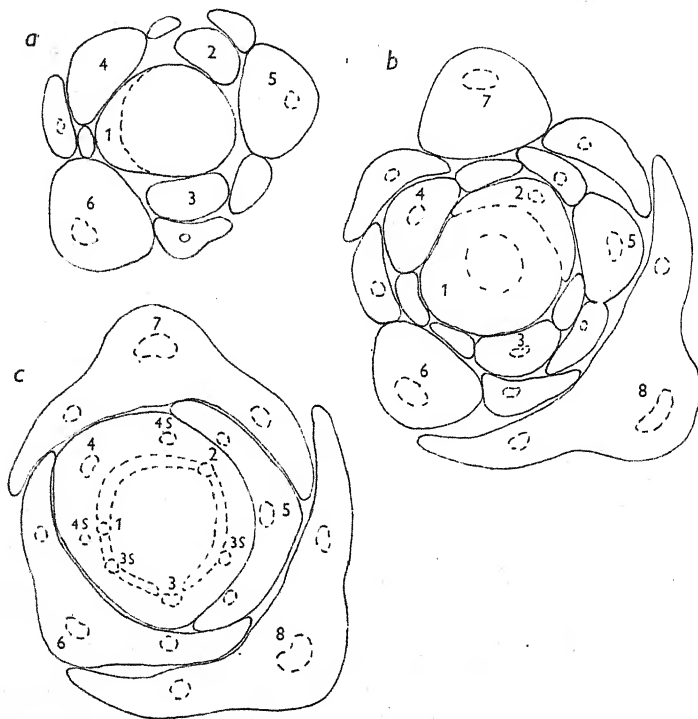


Fig. 1*a, b, c*. *Lupinus albus*. Three sections of a normal apex. *a*, through the insertion of the youngest leaf primordium; *b*, just below it; *c*, lower again showing the median bundles and stipular bundles, marked *S*, in the stem. All $\times 56$.

a main median trace and two smaller traces from the stipules. These remain separate and continue to descend fairly straight until they unite with traces nearly directly below them belonging to the leaves two and three plastochrons older. The median bundle of any leaf n unites with the anodic stipular bundle of leaf $n-3$ after descending through about four internodes. But not far below the youngest leaves the traces become merged in a conducting ring through differentiation of the tissue between them (Fig. 1*c*).

The young leaves visible at the time of operation will be called as before P_1, P_2 and so on, P_1 being the youngest, and those still at that time due to arise will be called I_1, I_2 and so on, I_1 being the next leaf due.

In the experiments the young leaves overarching the stem apex were removed as before

* The Schimper-Braun fractional classification cannot be applied correctly to spiral phyllotaxis systems in buds, where the systems are formed, since it is based on the assumption that the mean divergence angles in different systems are simple fractions of 360° , or, as comes to the same thing, that exactly superposed leaves can be found. This assumption is completely untrue for the spiral systems of buds (see Snow & Snow, 1934, p. 136).

under a binocular dissecting microscope, until there remained only the four or five youngest, which do not hide the apex. Then with a very fine scalpel a horizontal cut was made into the apex just below the presumptive area of I_2 , or in one experiment, of I_1 . In order that the cut might pass just *below* the presumptive area and so not injure it directly, it had to penetrate the insertions of the two main contact leaves just below. These were P_1 and P_2 , the two youngest existing leaves, when I_2 was undercut, or P_2 and P_3 when I_1 was undercut. It will sometimes be convenient to call these leaves $n-2$ and $n-3$, the undercut presumptive area being then called n . So far as could be judged the cut was made deep enough to sever the region presumptive for the median trace of the undercut leaf. After 12-14 days the apices were fixed in alcohol, embedded in collodion, sectioned transversely and mounted in glycerine 66%. The seedlings tended to flower too early, unlike any of those grown previously, and consequently some had to be rejected, and even in some of those illustrated the upper sections are made more complicated by the large axillary buds which are formed towards the flowering stage. The sections were drawn and were examined to discover exactly how far the wound had penetrated and at what level, and how the undercut leaf had developed. The level of the wound could be seen in relation to the insertions or basal areas of the leaves $n-2$ and $n-3$, just below the undercut presumptive area of leaf n .

Our reason for choosing usually to undercut I_2 was that this presumptive area is not yet in any way determined to form a leaf in this species, a statement for which the evidence has been fully set out and explained previously (1933, p. 398; see also § 4 below). Even an early I_1 is not determined, but determination takes place at some time between the beginning and the latter part of the I_1 stage, that is, of the last plastochron before a leaf arises. We shall therefore include the result of one undercut of an I_1 which was at an early stage of the plastochron, as was shown by the small size of P_1 .

The results were the following. In a few preliminary experiments the wound was found to have reached too high, up to a level above the insertion of leaf $n-2$, so that the presumptive area of leaf n must have been cut into. These experiments, which led to various abnormalities, must therefore be rejected, and so also must be some in which the wound had not been made deep enough to disturb the conducting ring. But there remain to be considered seven apices, of which five are illustrated in Figs. 2-6, six of the seven with I_2 undercut and one (Fig. 4) with an early I_1 undercut. In these apices it was seen that the cut had certainly penetrated the region from which the median leaf trace of the undercut presumptive area was due to be differentiated, and yet there had subsequently arisen from that area a leaf which was just about of the normal size in relation to the other leaves, and at just about the normal angular position. This leaf was also inserted at just about the normal level in five of the seven apices, but in the other two, those shown in Figs. 3 and 4, it was inserted slightly higher than the normal, being nearly at the same level as the next leaf along the genetic spiral, so that it must have been slightly delayed. In these two apices the wound was found slightly higher up than in the others, reaching to the very top of the insertion of leaf $n-3$ or just above it; so probably in these two the wound had encroached slightly on the undercut presumptive area itself, and thereby had slightly delayed the leaf due to arise from it. In the other five experiments, the level of the top of the wound was found to be somewhere within the insertion of leaf $n-3$ (that is, of P_2 in these apices) and since this leaf is immediately below the undercut presumptive area, the cuts even in these apices must have been very close below that area.

The wounds appeared in the sections as disturbed regions of irregular tissue, often containing patches of wound scar or bits of strands of wound tracheids, but not as gaps, since the gaps made by the cuts had healed up. This was probably due to outgrowth of new tissue from their inner margins, since cuts made into stem apices gape and do not heal by direct union of the cut surfaces unless compressed. Within the disturbed region the normal tissue of the conducting ring was lacking, though there were in some places some patches of very weak and irregular conducting tissue, which are outlined in the figures by dots. The normal median trace of the undercut leaf could be followed downwards to the wound region and seen to end there in six of the apices, and in the one shown in Fig. 2 to be continued only by a very weak and devious regenerated strand. Figs. 5*b* and 6*b* show the median bundle of the undercut leaf (I_2) in the stem just above the wound region (Figs. 5*c*, 6*c*) in which it disappeared.

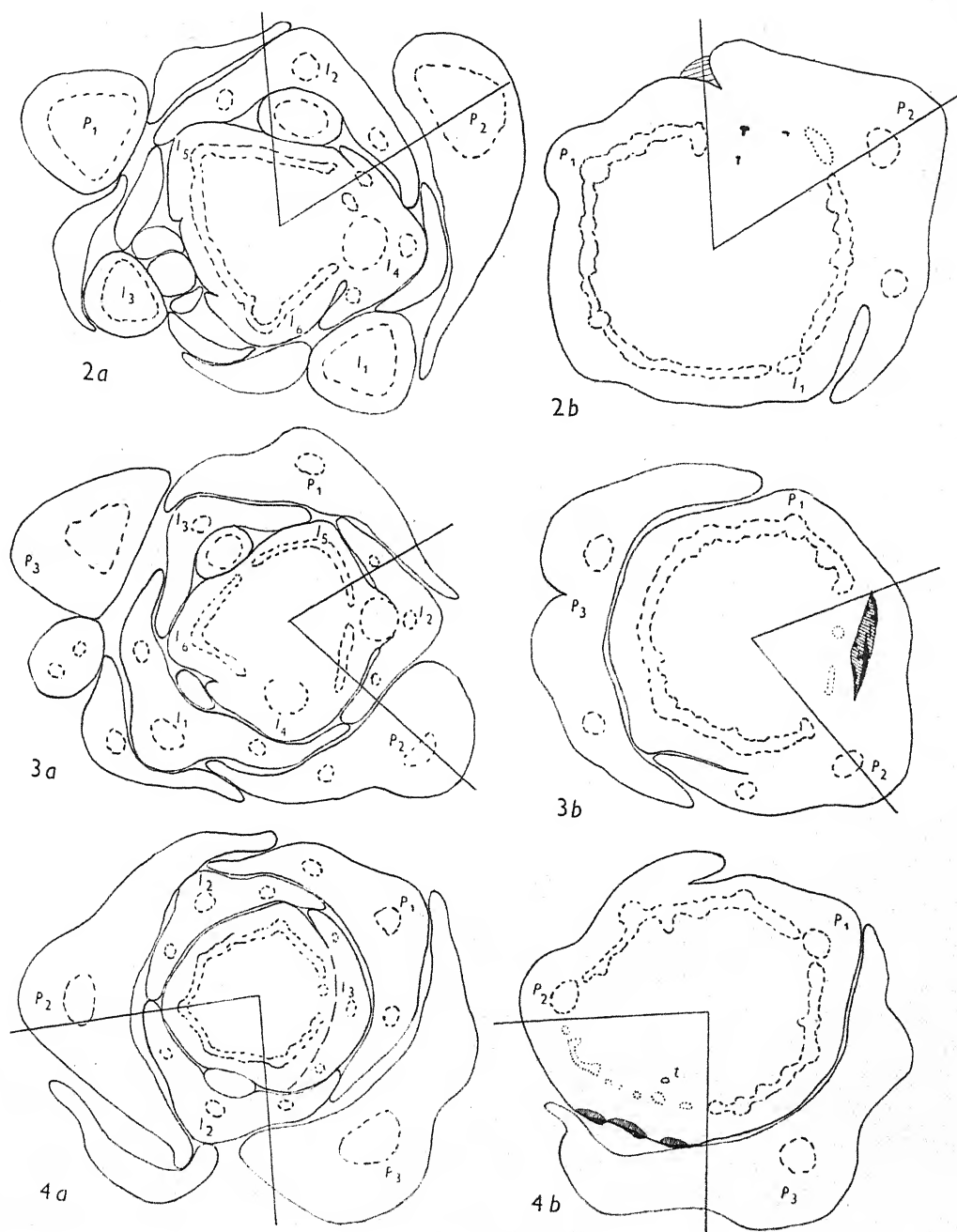
The interpretation can only be that the cuts had penetrated the tissue from which the traces and conducting ring were due to be formed; and that at some later date the gaps made by the cuts had become filled up with regenerated tissue through which, later again, new conducting strands were just beginning to be formed.

In the figures the region within which the conducting ring had been penetrated by the cut and weakened in this way is marked out by the lines of a sector drawn on the section of each apex made at wound level; and the same sector has been projected on to the higher section, so as to show the size and position of the cut in relation to the undercut leaf. This was done by first drawing on the lower section the median line of this sector (not shown in the figures), measuring its angle from the centre of a neighbouring leaf and then transferring it to the higher section. It can be seen that the breaks in the conducting rings due to the wounds all underlie the centres of the undercut leaves and much of their lateral parts also. The angles of the wound sectors range from 63 to 94°, and in the two apices not illustrated they were 63 and 46°. The sections have not been photographed, since being unstained they would not show up well.*

A large part, therefore, of the tissue immediately below the undercut presumptive area, including the tissue from which its median bundle was due to be differentiated, must have been completely interrupted by the cut for a considerable period in each of the seven apices; and the formation of conducting strands across the region of the cut, when this region became filled up, was so long delayed that it was only just starting 12 or 14 days later, six plastochrons or more after the undercut leaf had arisen. In spite of this the undercut leaves, as already stated, were all about normal in size and angular position, and in five apices they were at just about the normal level, though in the other two, as stated, they were inserted slightly higher, probably because the cuts were slightly higher, as could be seen.

For comparison it may be recalled that our earlier experiments on this species (1931, 1933, 1937) showed how readily and drastically the positions in which leaves arise can be changed by changes in factors which really do affect those positions, for instance by cuts, even quite slight, made actually in their presumptive areas, or indirectly through changes in the positions of neighbouring leaves, or by local applications of auxin. In comparison with these earlier results the present results surely show beyond doubt that in this species leaf traces and the tissues from which leaf traces will be formed play no appreciable part in

* We hope to exhibit the sections at a meeting of the Society for Experimental Biology at Oxford in July 1947.



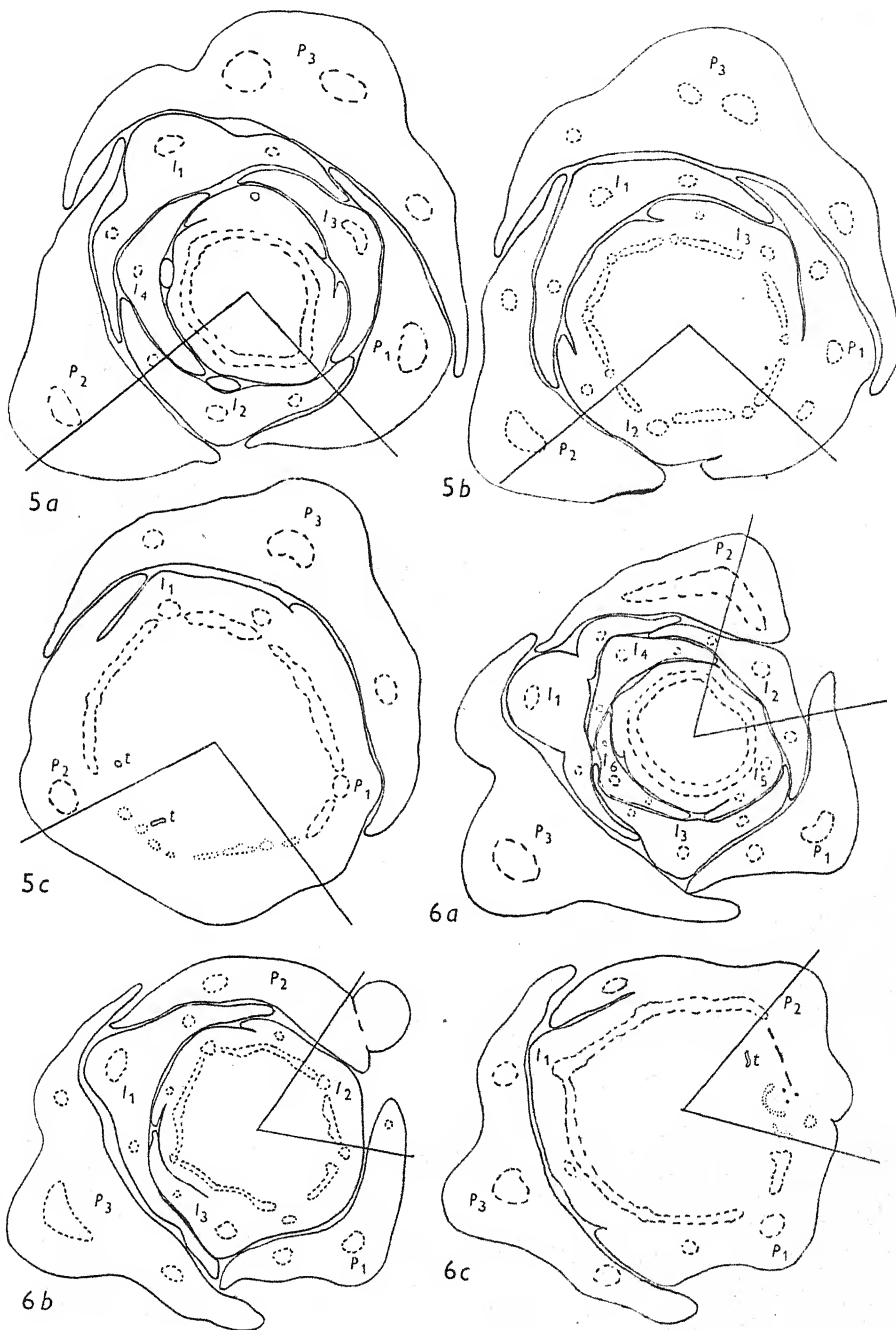
Figs. 2a, b; 3a, b; 4a, b. *Lupinus albus*. Three apices in which the presumptive area of I_2 or I_1 was undercut. On the lower section *b* of each apex the extent of interruption of the normal conducting tissue by the wound is marked with a ruled sector, and this sector is projected on to the higher section *a* which shows the undercut leaf. Wound scar is shown black, injured and moribund tissue is hatched, wound tracheids are marked *t* and weak regenerating conducting strands are outlined with dots instead of the broken lines used for normal strands. All $\times 34$.

determining the positions of the leaves. Naturally it remains possible that they may do so in some other species, but it seems unlikely that other species differ in so fundamental a point.

Evidence tending in the same direction has been provided by Wardlaw (1945^b, 1947), who made vertical tangential cuts all round the large and rather flat stem apices of a fern, *Dryopteris aristata*, just above the top cycle of leaf primordia, so as to sever the conducting zone or incipient conducting zone, which in these ferns reaches very far up. The apices beyond the wounds went on growing and forming leaves, apparently at about the normal rate, and also new conducting tissue. But though these experiments are valuable, they were designed for studying not problems of phyllotaxis, but various other problems, as Wardlaw states (1947, pp. 345, 352), and they do not conclusively disprove a determination of leaves by traces for the following reasons. First, it is not known when in ferns the presumptive areas on the stem apex are determined to form leaves, so that some of those areas above the cuts may have been determined already. Secondly, Wardlaw gives reasons (1947, p. 352) for thinking that in some of the experiments regions of tissue that were already determined to form parts of the conducting system were left on the apical sides of the cuts. These parts therefore when differentiated might have determined the leaves above. Also the method of cutting all round the stem apex does not make it possible to test by comparison of leaves in one apex whether leaf formation is delayed, even if not prevented. Wardlaw promises further attention to problems of phyllotaxis. A nearly similar experiment with similar result is reported briefly by Frazer (1946).

But whereas leaf traces do not determine leaves in *Lupinus albus*, there is plenty of evidence that the young leaves promote the growth of their own traces in this species, as Helm (1932) showed by experiment for other species, and as Wardlaw (1947) has concluded for ferns. For whenever in our experiments leaves were caused to arise in quite abnormal positions, their traces were always formed beneath them as usual; and it is not credible that the positions of the leaves and traces were always changed by the operations similarly but independently. Also in the present experiments, as already stated, the median trace of the undercut leaf descending in the stem terminated at the wound region, except for a feeble regenerated continuation in the apex shown in Fig. 2.

It may, however, be asked how it is possible, if traces do not determine leaves, that in *Sequoia sempervirens* and probably in *Ginkgo biloba* the traces are formed well before the leaves and in positions that are usually in regular order beneath them, though apparently not always so in *Sequoia* (Sterling, 1945). The following answer may be suggested. It is probable, from comparison with other species, that even in those species in which the rudiments of the traces are formed first, the leaves when they arise later greatly promote the differentiation of those rudiments. It may then be supposed that in these species the rudiments of the traces, when their differentiation has been promoted by their leaves above them, tend to give off branches upwards according to some rule, perhaps into each space between the existing traces in turn as soon as it becomes wide enough (cp. Sterling, 1945, p. 385); and this suggestion could perhaps be tested by experiment. If, then, the traces are successively strengthened by the leaves above them which arise, as we believe, successively in each gap between existing leaves that becomes available, and if the traces then give off branches according to some rather similar rule, then those branches will very probably come in regular order beneath the positions of future leaves.



Figs. 5a, b, c; 6a, b, c. Two more apices in which the presumptive area of I_3 was undercut. The sections b show the median trace of the undercut leaf in the stem just above the wound (section c) where it terminates. Fig. 5, $\times 37$; Fig. 6, $\times 28$.

3. THE THEORY THAT THE DERMATOGEN GROWS EXCESSIVELY AND SO MAKES FOLDS

The theory to be discussed in this section was proposed by Schuepp (1914, 1917). He based it on counts showing the index of division—that is, the proportion of cells that are dividing at any time, in the dermatogen and in the interior of the stem apex of *Lathyrus latifolius* (1914, p. 335)—and he believed that this index was a trustworthy measure of the rate of growth, a belief which seems to us open to question in spite of the facts which Schuepp cited to support it (1914). The index of division was about the same in the dermatogen as in the interior, but in the dermatogen the divisions are at right angles to the surface and the growth therefore tangential, whereas in the interior they are in all directions. From this Schuepp calculated that the dermatogen must grow tangentially too fast for the interior and so begin to throw itself into folds, and this he considered to be the first stage in the formation of a leaf. This theory was accepted by Priestley (1928, p. 8). Schuepp also stated (1914, p. 338) that the transition from the manner of growth of the dermatogen to that of the interior is not sudden but gradual.

It is thus essential to Schuepp's theory that the dermatogen of the stem apex should be compressed tangentially by its own growth; and if so, a slight cut made in the apex should tend to close up. It should do so especially strongly if the next layer or two towards the interior is also somewhat compressed tangentially, as would follow from Schuepp's statement that the transition in manner of growth is gradual. But even if only the dermatogen is compressed, a cut should still tend to close up, since the pressure is supposed to be great enough to raise up the dermatogen in spite of the resistance of the internal tissue to which it is attached.

Now one can observe under a dissecting microscope whether cuts in stem apices close up or gape, and we had already done so incidentally when operating for other purposes. But in order to test Schuepp's theory, we thought it worth while to make such observations more deliberately and thoroughly in the best possible conditions. We made our observations on seedlings of *Euphorbia lathyris* and shoots of *Dahlia variabilis* just sprouting from tubers, since these two species have much the largest apices of any that we have yet tried. *Euphorbia lathyris* has the further advantage that it does not flower in its first year, and that its leaves are simple and narrow so that the apex can be very quickly and easily exposed; it can be strongly recommended as a very easy plant for operations on stem apices. The seed must be sown when ripe to germinate next spring. Both species have decussate phyllotaxis. The plants were all well rooted in pots and growing rapidly when operated upon. We found it necessary for good observation that the light should be well diffused so as to prevent glittering reflexions, and that the apices should not become moistened with sap exuded from the cut leaves. The apices and the whole plants were, however, quite turgid at the time of the operation. We used a Leitz 'Greenough' binocular magnifying 72 times and a very fine pointed cataract knife. The light was cooled by passing through water. After exposing the stem apices we made slight cuts in them either in a radial vertical plane or in a transverse plane, and in the presumptive area either of an I_1 or of an I_2 . The total of cuts, usually one to an apex, was the following: in *Euphorbia* two vertical cuts and one transverse cut into I_1 , and the same number of each into I_2 ; in *Dahlia* four vertical cuts into I_1 , and one transverse cut into a part of the stem apex not recorded. The cuts all gaped immediately and widely. Some of them were drawn and are shown in Figs. 7 and 8. Also when two apices of each of these species were split right through, the halves diverged immediately (Fig. 9).

In earlier experiments in which apices of *Stachys silvatica* and *S. tuberifera* received slight radial vertical cuts in an I_1 for another purpose, it was noted that the cuts regularly gaped at once. But these apices are very much smaller, and the exact details therefore less easy to see. Also so far as we remember, in the previous experiments on *Lupinus albus* (1931, 1933) the cuts made into the stem apices always gaped.

These simple observations show that in growing vegetative stem apices the dermatogen and the next few cell layers are not compressed, but in tension tangentially in both directions. So the tissue tensions in these apices are similar to those in the older parts of

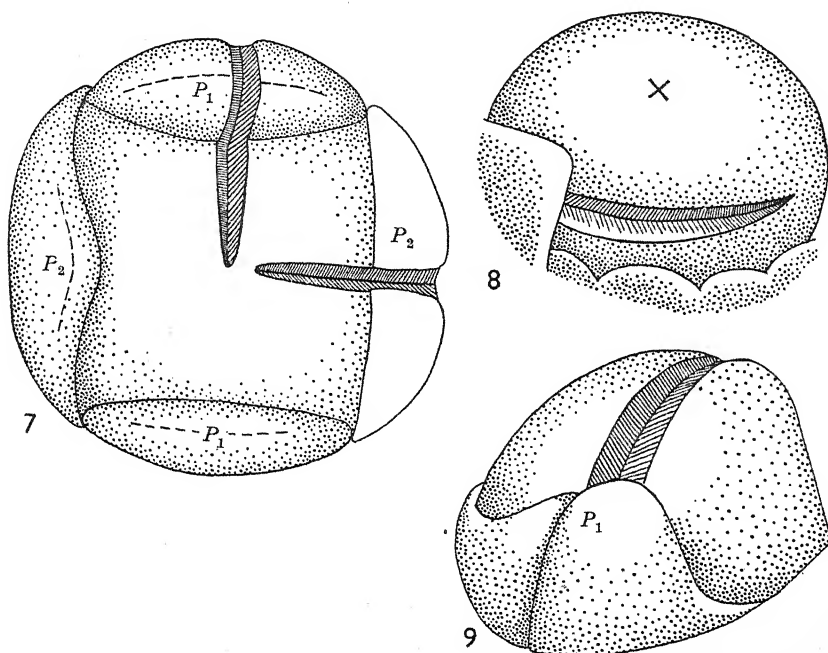


Fig. 7. *Euphorbia lathyris*. A stem apex seen obliquely from above with two gaping radial cuts. One cut is in the site of an I_2 and also passes through a P_1 primordium below: the other is in the site of an I_1 and passes below through the base of a P_2 that has been cut down and is shown unshaded. The summit ridges of primordia are shown with broken lines.

Fig. 8. *Dahlia variabilis*. A stem apex seen obliquely from above with a gaping transverse cut. The summit of the apex is marked approximately with a cross. The tips of various young leaflets are seen below.

Fig. 9. *Dahlia variabilis*. A stem apex seen obliquely from above after being split right through. The cut has also split a P_1 primordium: the opposite P_1 is hidden.

stems, of which the halves diverge when split, though flowering apices need to be studied separately. A theory of leaf formation therefore which is based on the assumption that they are compressed tangentially must be incorrect. Such a theory could not anyhow apply to leptosporangiate ferns, as Wardlaw has pointed out (1945a, p. 107), since in them a leaf develops from a single cell before anything like a fold is formed.

It seems also of interest to record for comparison the results of cutting into the young leaf primordia. In *Euphorbia lathyris* when vertical cuts were made into their outer or abaxial faces, the cuts did not gape, or practically not at all. This was noted twice after cuts into a P_1 , four times after cuts into a P_2 and once each time after cuts into a P_3 and

a P_4 . These results are not illustrated since there was practically nothing to see, though the tip of the knife had been clearly seen to enter the tissue. They contrasted strikingly with the results of the cuts into the stem apices and served as a useful check on them.

In *Dahlia* the results were a little less consistent, since out of six cuts made into the outer faces of P_1 primordia, though three again did not gape, yet one gaped distinctly and two slightly. But in *Dahlia* also the gaping was on the whole much less than after the four cuts into stem apices, which all gaped widely.

However, in both species when a P_1 was split completely through, either in a radial or a tangential plane, the halves usually diverged. The split P_1 shown in Fig. 9 is one of the few in which the halves did not diverge, and in this one they did round off, so that the line of the cut showed clearly nevertheless. The tissue tensions of young primordia need further study.

4. THE REPULSION THEORY AND THE THEORY OF THE FIRST AVAILABLE SPACE

We propose to give the name 'repulsion theory' to the theory that each new leaf arises at the greatest possible distance from the slightly older leaves which form the uppermost cycle round the apex. Suggestions of this kind were made by Schmucker (1933) and by Priestley & Scott (1933), who wrongly attributed the same idea to Hofmeister (1868); and the idea has probably occurred at some time to most people interested. Different from this is the theory for which we claim to have produced evidence previously (1931, 1933, 1935), that each new leaf arises in the first available space on the apex above and between the existing leaves or other contact members in the top cycle—that is to say, in the first space which attains both some necessary width and some necessary distance below the extreme growing-point. But we suspect that this theory, which is based on the ideas of Hofmeister (1868) and van Iterson (1907), is often confused with the repulsion theory, and we therefore think it worth while to set out again the evidence which, as we believe, makes it possible to decide between these theories: for it is probably by so doing that we can best make clear the difference between them. Some of this evidence we have already repeated briefly (1934) in relation to the theory of Priestley & Scott (1933), but it will be best to set it out here in relation to repulsion theories in general rather than to any one form of them.

On the repulsion theory the exact position in which a new leaf will arise must depend on influences exerted by *all* the existing young leaves in the top cycle round the apex at the least. But on the theory of the first available space the expectation is different. Around the apex there are a number of depressions or gaps between the leaves of the top cycle, and these gaps become available successively and are occupied by new leaves. So the sequence in which the several gaps are occupied by new leaves does depend on the positions and shapes at any time of all the existing leaves of the top cycle. But the exact position *within* any one of these gaps in which a leaf will be formed depends on the positions and shapes of those leaves only which border the gap, and not on the other leaves of the top cycle. Now in a spiral system with contacts 2 and 3, the existing leaves which border the gap in which a new leaf n will arise are the leaves $n-2$ and $n-3$,

whereas the leaf $n-1$ does not border that gap nor make contact with leaf n when it arises. Consequently, if in this system one changes by an operation the position, size or shape of a leaf n or of its presumptive area, and if the operation does not change the sequence in which gaps become available for the next few leaves, then the exact position of leaf $n+1$ (the next younger leaf) within its gap will not necessarily be changed on the theory of the first available space; but the position of leaf $n+2$ will be changed, since it normally makes contact with leaf n . On the repulsion theory, however, the position of leaf $n+1$ should also always be changed, provided that it is not already determined. Thus the position of leaf $n+1$ can decide between the two theories.

In *Lupinus albus* the system is effectively this system with contacts 2 and 3, since the stipular contact 1 is very slight at the early stages and makes little difference. Also our operations on a young leaf or on its presumptive area (1931, 1933) usually did not change the sequence in which the next two gaps became available, though they often changed the sequence of subsequent gaps; and consequently these operations serve to test the two theories. We found actually that operations on a leaf n or on its presumptive area did not appreciably change the position in which leaf $n+1$ arose, except in certain experiments mentioned below in which an abnormal leaf arose very soon after the operation and encroached upon the space normally occupied by leaf $n+1$. But leaf $n+2$ was regularly much displaced. Thus when I_1 , the presumptive area of the next leaf due, was isolated from the apex by a vertical tangential cut, the position of I_2 in relation to the leaves with which it made contact below was never noticeably changed; but I_3 was always found to be displaced towards the wound, whenever its position in relation to the leaves below it could be seen accurately (1931, p. 17 and Table 2). Yet I_2 is not determined at the time of operation, since when P_1 , the youngest visible primordium, was similarly isolated, then I_2 was usually displaced towards the wound, like I_3 after the isolation of I_1 (1931, Table 1).

Again when I_2 was isolated, then in twelve out of twenty-one apices I_4 was strongly displaced towards the wound, but I_3 was not noticeably displaced (1931, p. 27). One of these apices (no. 132 of Table 3, 1931) is illustrated here in Fig. 10. The unchanged position of I_3 is clear from the normal relation of its median bundle to the stipular bundle of P_1 . The displacement of I_4 towards the wound is obvious, though less than in any of the other apices of this group. But in the other nine apices in which I_2 was isolated, another leaf which we called I_2' , difficult to compare with any normal leaf, arose somewhere above the wound before I_3 and extended one edge into the presumptive area of I_3 . So naturally in these apices I_3 was displaced in consequence.

Results similar in principle were obtained after the operation of splitting I_1 in a radial vertical plane (1933, pp. 369, 377). Full details and many illustrations of the above results were given previously.

Further evidence against the repulsion theory is provided by the results of some of our experiments in which at some time after the operation the stem apex came to be encircled by two leaves only, of which one or both were asymmetric at their bases (see Fig. 10c and d, I_3 and I_4). The morphological centres of these leaves, marked by their median bundles, were nearly but not quite opposite, and the asymmetry was such that the larger side of one or both of the leaves was on that side of the apex on which their centres were separated by the larger angle—more than 180° . Consequently on that side these leaves occupied more of the surface of the apex and there was more space left available on the other side of the

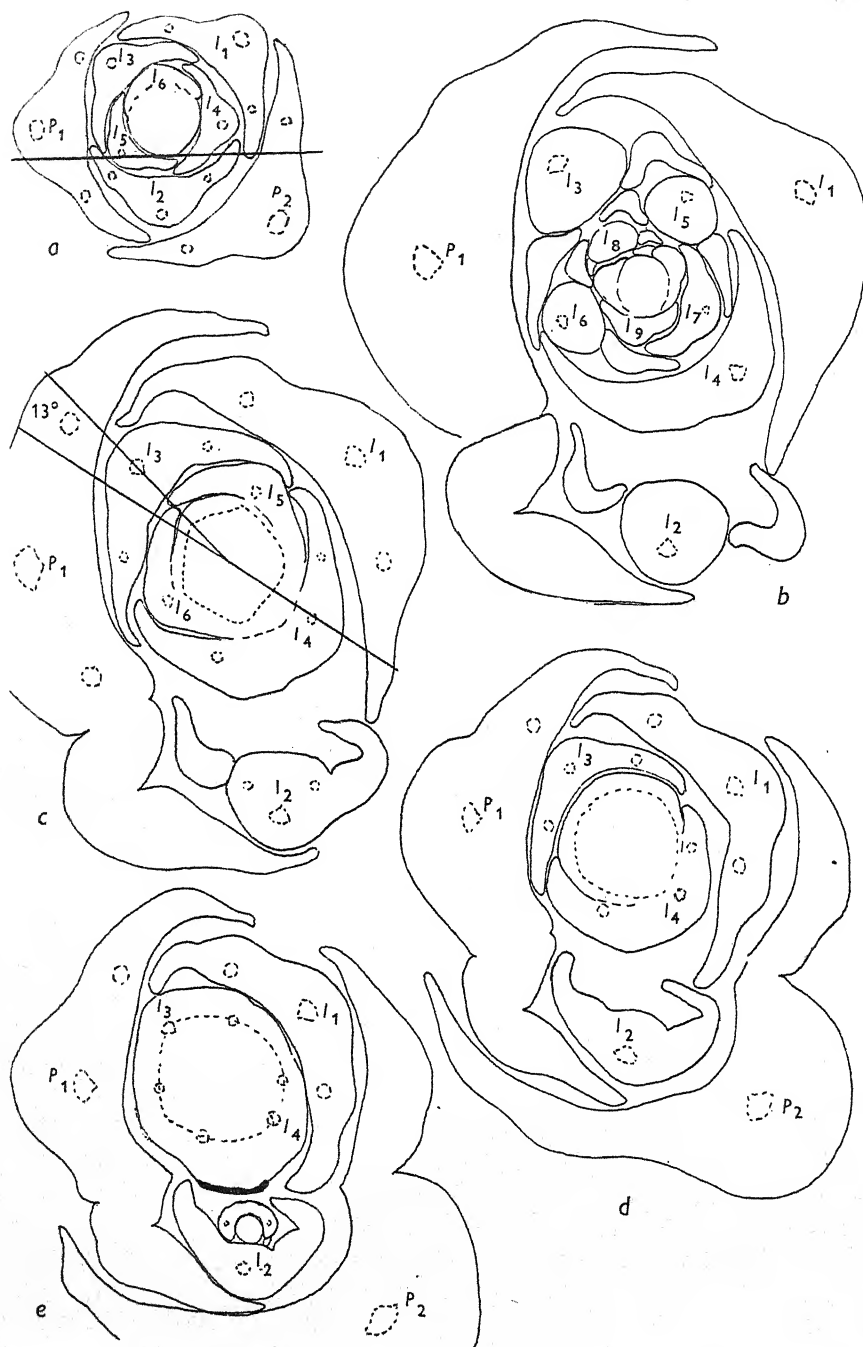


Fig. 10. *Lupinus albus*. Sections *b* to *e* are of an apex in which I_2 had been isolated. Section *a* is of a normal apex with a line in a position corresponding to that of the cut. Wound scar is shown black in *e*. *b* and *c*, $\times 44$; *d* and *e*, $\times 33$.

apex, where the angle between the morphological centres of the leaves was the smaller. Three of these experiments were isolations of I_1 (1931, p. 9 and Fig. 7) and four were radial cuts through I_1 (1933, pp. 383, 396 and Fig. 15). Another, not previously illustrated, was the isolation of I_2 shown here in Fig. 10. In all of them the next leaf arose on that side of the apex on which the space left available by the edges of the two previous leaves was the larger, although the angle between their median bundles was the smaller.

In the apex shown in Fig. 10 the spiral reversed in consequence. Sections *b* and *c* of Fig. 10 are rather oblique, but the sequence of I_5 and I_6 is clear from the outlapping of I_6 by I_5 .

These results indicate that the determination by existing leaves of the position of the next leaf depends on the way in which they occupy the surface of the apex with their bases rather than on any physiological influence such as is assumed on the repulsion theory; for any such influence would be expected to come mainly from their main central bundles. This is indicated also by the fact that the positions of leaves are determined in a similar way by quite other objects, for instance by cotyledons and in the experiments by the areas occupied by the wounds. These results and observations are thus opposed to the suggestion of Gunckel & Wetmore (1946*b*, p. 540) that determination of leaf positions by spatial relations may take place deeper down in the region of the traces, as well as near to the surface of the apex.

On the theory of the first available space one need not assume any special causes of leaf formation acting at any special positions on the apex; for all the superficial tissue of the apex is supposed to tend to form leaves as soon as it has undergone the changes involved in moving downwards far enough from the extreme tip. But the determination and formation of a leaf is supposed to need some minimum available space, and in this way the position of each leaf is determined. For this assumption we offered direct evidence previously (1933, p. 396), and we also discussed the difficulty concerning the effects of aborted leaves (1933, p. 398). We agree that in some species with phyllotaxis systems of other than the usual spiral kinds other factors determining leaf positions come in besides the space-occupying process, for instance, in many species with whorled phyllotaxis (Snow, 1942) and in ridge-forming succulents (Weisse, 1904).

The idea of a minimum space necessary for determination is supported by some experiments reported in a remarkable and very original work by Magnus (1906) on regeneration in mushrooms. In normal development the rudiments of the gills are formed in a ring, and, as the margin of the cap grows radially, so the rudiments grow radially after it and form the regular gills. But after some of his operations, the young fruit bodies formed a considerable wound tissue on which gill rudiments later arose simultaneously over the whole surface (p. 95), so that most of them could not make regular radial growth but grew quite irregularly into pegs or short, curving ridges. Yet even here measurements and counts in several directions showed that the rudiments had a fairly constant breadth, between 0.07 and 0.1 mm. and never less, and were nearly but not quite touching. So any point on the surface of the wound tissue was capable of forming a gill rudiment, but it did so only if a certain minimum space was available, as Magnus himself concluded (pp. 98, 127). Further details must be found in the original. Magnus even suggested that a similar idea might well be applied to phyllotaxis and tested experimentally (pp. 125 seq.), and he made some instructive comparisons with leaf formation, especially concerning the determination of a primary area before a rudiment arises from it (p. 128).

SUMMARY

1. Evidence is offered and discussed relevant to three current theories of leaf determination or formation. The first of these is that leaf traces determine the leaves above them, the second is that the superficial layer or layers of the apex are tangentially compressed by their own growth and so form folds, and the third is that a new leaf is repelled by the existing leaves of the top cycle and so formed at the greatest possible distance from them.

2. In *Lupinus albus* transverse cuts made into the apices close beneath the presumptive area of I_2 , the next leaf but two, or of I_1 , and deep enough to sever the region presumptive for its main trace were found after from 12-14 days not to have appreciably delayed the formation and growth of that leaf, nor to have altered the angular position in which it arose. Yet regeneration of conducting tissue through or round the wound had scarcely started. Since, therefore, I_2 is not yet determined (Snow & Snow, 1931, 1933), it follows that in this species at least traces do not determine leaves at all.

3. In the stem apices of *Euphorbia lathyris*, *Dahlia variabilis* and other species, slight cuts made in any direction gape at once. Also the halves of split apices diverge at once. The superficial layers are therefore in tension tangentially and not compressed, and the second theory is untenable.

4. On the repulsion theory the exact position of a new leaf should depend on influences exerted by *all* the leaves of the top cycle. Evidence from earlier experiments on *Lupinus albus* (Snow & Snow, 1931, 1933) shows that this is not so; for the exact position of a new leaf n within the gap which it occupies depends only on those existing leaves which border that gap, and not on leaf $n-1$, the next older leaf, which does not border that gap. Also the determining effect of the bordering leaves depends on the contours of their bases and not on the positions of their main bundles. These conclusions tell against the repulsion theory and in favour of the theory that each leaf arises in the first available space (Snow & Snow, 1931).

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THE BIOLOGY AND DEVELOPMENTAL MORPHOLOGY OF THE SHOOT APEX IN THE GRAMINEAE

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(With Plates 1-4)

The internal architecture of the grass shoot apex has been fairly thoroughly investigated,* but although certain features of the external morphology have been described,† a broader study is needed, particularly from the point of view of what may be termed the biology of this region. In the present study, the morphological changes which the apex undergoes during its ontogeny are followed in dissected material of *Agropyron repens* (L.) Beauv. and the observations later used to elucidate some of the features commonly seen in various types of grass shoots. It is hoped that the investigation may also have a wider application in throwing light on, for example, problems such as those raised by the interest now being shown in grassland management and in programmes of cereal and herbage grass breeding based on the production of fertile amphiploids from sterile hybrids by the use of colchicine, etc.

Agropyron repens was chosen because it provides an adequate range in apical morphology and also possesses a number of interesting features such as rhizomes, 'blind' shoots, etc. The choice was further influenced by an interest in *Triticum-Agropyron* hybrids, since it was felt that the present study has a bearing on the alternatives of annual, caespitose or rhizomatous habit which are bound to be considered if successful perennial wheats or superior wheat-couch grass forage types are to be obtained.

MATERIALS AND METHODS

(a) Dissection.

Contrary to expectation, it was found that, with a little practice, it is not difficult to dissect out the shoot apex in the grasses. The fascination of actually seeing the living apex with the newly initiated primordia in various stages of their early development amply repays any effort involved, and at the same time the method is ideal for building up a true mental picture of the three-dimensional shape of apices and primordia and the changes they undergo during growth. It is also a powerful corrective of impressions derived from the study of serial sections alone.

Except for a microscope (preferably a stereobinocular) to be used during the last stages of dissection and the examination of the apex when it is uncovered, the only apparatus needed is an ordinary mounted needle and a hand-lens held in a rigid support. For the latter, a large reading glass in a clamp stand is excellent because it leaves the hands free and, if of about 7 cm. diameter or more, allows both eyes to view the material during dissection; a pair of short-focus spectacles might perhaps be substituted. With regard to

* Douliot (1891), Bugnon (1924), Hsü (1944), Porterfield (1930), Rösler (1928), Kliem (1937), Sharman (1945 *a* and *b*).

† Deiniga (1898), Bugnon (1921), Bonnett (1935, 1936, 1937, 1940), Evans & Grover (1940), Noguchi (1929), Sharman (1942 *a*), Weber (1938, 1939).

the needle it is an advantage, but not essential, to convert it into a miniature knife by rubbing two sides of the tip on a hone.

When the shoots for dissection are being removed from a tillering clump, each should be detached from the rest of the material as low as possible because the apex is often situated much farther down inside the enclosing leaves than is at first sight imagined; merely cutting off a shoot usually only gives a tube of enrolled leaves. Starting with a selected shoot, the outer leaves can be removed without the use of a lens or a needle until the one with only part of its lamina exposed and green is reached. At this stage, in the vegetative shoots of most grasses, the position of the apex inside the remaining 'bud' will be about 1 cm. up from the insertion of this outer leaf. Now, with the material in one hand, the mounted needle in the other and with both arms relaxed and in contact with the bench as much as possible, the next three or four leaves are dissected off one by one under the hand-lens.

In the case of a species where the sheath has overlapping edges, these may be slightly unrolled before the needle is used to cut through the leaf insertion. When dealing with a type where the sheath is in the form of a closed tube, this should first be split down and then the base freed from the axis. After a little practice, at least the first one or two bud leaves can usually be removed without the aid of the hand-lens, which is found less and less necessary as skill is acquired, especially if a number of similar shoots of one particular species are being dissected; in fact, when dealing with a series of the later stages, the shoots may even be dissected straight down to the stage when they are ready for examination under the microscope.

A first trial can well be made with *Glyceria fluitans* R.Br. which is one of the easiest species to dissect because its leaves are conduplicate and contain little lignified material so that they cut cleanly and easily, in a manner curiously reminiscent of snow.

When the stem becomes difficult to hold, the base is inserted into a pellet of 'Aloplast' or 'Plasticine'; this small holder is also useful later because it can be moulded so that the apex will remain on the microscope stage in any desired position.

(b) Photography

When an apex was to be photographed, it was placed (the stem still enclosed in the holder) in a dish of clean tap water for about 20 min. This allowed it to become fully turgid and thus better able to withstand the intense lighting which had to be employed.* After soaking it was placed on a piece of moistened black paper inside a cell about 3 cm. high covered by a large microscope slip. The whole was placed on a glass plate so that it could be moved easily when being examined under the microscope or camera. The cell was made from a strip of cleaned X-ray film and of such a height that the coverslip was so completely out of the focal plane that it could be left in position during exposure. The apices were illuminated by a lamp taken from a sub-standard cine projector and the photographs taken with a Leitz 'Makam', used on one side of a binocular microscope, at a magnification of $\times 45$ on the plate.

At first considerable difficulty was experienced because the intense illumination soon damaged the apices and at the same time caused them to move out of focus during

* A cuticle or similar covering seems to be present even over the cells of the extreme tip, for after immersion undamaged apices only retain water by capillarity between the older leaves at the base. Any adhering here may easily be removed by gently touching this region with the torn edge of a strip of filter paper.

exposure. The insertion of a tube of copper sulphate solution to absorb the heat of the illuminating beam considerably lengthened the life of the apices and also reduced their movement a little. This latter difficulty was minimized by dimming the lamp by means of a resistance during preliminary focusing and only using the intense light for the quick final adjustment and the exposure itself. The effects of the movement were lessened by the use of very fast plates to reduce the time of exposure, but there were limits to which this could be followed since such plates tend to give a coarse grained image which is also undesirably soft; even as it was, in spite of the use of a contrasty developer and employing this under constant agitation, the negatives generally had to be printed on contrasty or extra-contrasty paper. Occasionally negatives were sepia toned in an effort to increase their contrast.

GROSS MORPHOLOGY

(a) *Rhizomes and aerial shoots*

In any given area, in, for instance, a recently dug plot, almost all the plants of *Agropyron repens* have come from pieces of rhizome; the production of grains and consequently of seedlings is infrequent in this species. At intervals of 2-4 cm. the rhizome bears reduced leaves which usually have the structure of sheaths throughout their lengths.* Occasionally, however, cases may be found where a ligule occurs about 2-3 mm. from the extreme tip, so that something approaching a miniature lamina is present. Where the scale leaves are separated from each other by appreciable distances, as on the vigorous horizontally running rhizomes, they usually appear double at first sight because their ends are split. Presumably this is caused by the forward growth of the younger leaves and their associated internodes.

When the rhizome reaches the soil surface, the leaves no longer develop into scales, nor do the internodes associated with the first aerial leaves reach more than about 0.3-0.5 cm. in length. The first aerial leaf is often a transitional one, consisting of a sheath bearing a reduced lamina about 0.25-1.5 cm. long. The next (second) aerial leaf usually bears a normal lamina about 10 cm. long, but it too may occasionally be of the transitional type.

Each successive aerial leaf has a longer lamina until about the third from the inflorescence is reached, when there is a slight progressive decrease. Counting the transitional leaf as the first, the main axis usually produces ten to eleven green leaves in all. In spite of the fact that practically all the plants were growing in the same neighbourhood, it seemed incredible that there could be any such constancy since presumably all the plants could have commenced their aerial development at different times. However, numerous observations spread over four years indicate that while there may be some slight variation, in this latitude at least, about 80% or more of the main shoots conform to these numbers.

(b) *Buds and branch development*

Buds are found in the axils of all the scale leaves on the rhizome but not all grow out, and of those which do the majority only do so at the beginning of the next season, long after the subtending scales have matured. They only produce new rhizomes, though there

* Since lamina and sheath are probably only of immediate physiological origin and are not good morphological units (Sharman, 1945 b) it would be wrong to think of the scales as 'leaves which have lost their laminae'.

seems to be some variation in the distance these grow before they commence to turn upwards towards the soil surface.

Buds may be found in the axils of the transitional leaf (leaf 1) and the next four green leaves, but they do not usually develop in the axils of any of the five higher leaves (nos. 6 to 10), nor in fact can even their rudiments be found here when shoots are dissected, a point which will again be mentioned later. The bud in the axil of the transitional leaf usually gives rise to an inflorescence branch of its own. That in the axil of the next leaf (leaf 2) may also do the same but usually this and the one in the axil of the third leaf develop into what may be called 'blind' shoots, each consisting of a succession of leaves associated with elongated internodes so that it becomes elevated and appears at first sight rather like a precocious flowering culm. Pl. 4*b* shows shoots of this type. There appears to be no limit to the number of leaves such a shoot may produce, but its growth is progressively slower as the season advances and by about mid-summer it has practically stopped. Similar blind shoots are produced if the buds in the axils of leaves 4 and 5 grow out, though they and even the one in the axil of leaf 3 may remain dormant.

APEX MORPHOLOGY

(a) *Rhizome*

Pl. 2*a* and *b* show two views of the same apex from a horizontally growing rhizome, after the adult scale leaf enclosing the terminal 'bud' and three more younger scale leaves have been removed. In Pl. 2*c* it is again seen after removal of the cowl-shaped next primordium (that seen at the base in Pl. 2*a* and *b*). The apex tip is now properly revealed and the first and second youngest primordia seen inserted a short distance back, though by now the apex and primordia are suffering from the dissection and illumination.

(b) *Aerial shoot*

By the time two or three aerial leaves have been fully expanded, the apex has become somewhat longer (Pl. 2*d* and *e*) and bears three to five primordia in successive stages of development. Whether at the apex of a rhizome or a young or mature aerial shoot, each new primordium first appears as a slightly raised protuberance some distance back on the flank of the apex. The up-pushing quickly spreads laterally to form a crescent partly encircling the axis and finally develops into an almost ring-like structure. Growth at first is mainly at right angles to the axis surface but soon a more vertical trend appears, as result of which, coupled with the fact that growth is always most rapid in the region of earliest initiation, the primordium changes firstly into a collar and then into a cowl or hood-shaped structure which grows up over the apex to enclose it and the new primordia which have since been initiated. This sequence of events may be followed by examining the stages shown in Pl. 1 in the order *i*, *o*, *e*, *g*, *f* and *d*. About the time the primordium is overtopping the apex, its edges grow over each other at the insertion, so that in the mature leaf the *extreme* base of the sheath is closed and tubular. By now growth of the young leaf is extremely rapid, so that only about two plastochrones* later the tip will begin to appear from within the enrolled leaves of the 'bud', and after this only an additional one or two plastochrones will be needed before it is exposed right down to the ligule and the lamina now fully expanded.

* The interval between the initiation of two successive leaf primordia is termed the plastochrone. Since individual shoots may be growing at different rates in terms of true time, it provides a useful 'morphological-time' unit for the chronology of events in the bud. For its use in this way, see Sharman (1942 *b*).

As the shoot becomes more mature, the apex becomes more elongated and the primordia are borne farther back from the extreme tip, Pl. 1 *f-l*. More primordia are seen in a closer series of developmental stages, but even here from the time one is about long enough to overtop the apex there are still only two to four (usually three) leaves between it and the first fully exposed one, so that in this case again the leaf still has only about three more plastochrones to complete its lamina development. It is as if, although the rate of final development (in terms of plastochrones but not necessarily in actual time) is constant, some such factor as a greater availability of 'food' leads to quicker initiation of primordia in more mature shoots and as a consequence allows older plants to maintain an increasing bulk of relatively meristematic tissue. The number of primordia found in the succession from the youngest discernible to the one which is just large enough to overtop the apex tip, gives a convenient scale for use in comparisons of apices of various lengths and is probably a rough measure of the amount of meristematic tissue being maintained. This index suffers from the obvious inaccuracy that a larger (and hence older) primordium will be needed to enclose a longer apex, but this objection is not so serious as it at first appears because by the time that the leaves are becoming hood-shaped and passing from the immediate region of the apex, they are elongating extremely rapidly.

Since in *Agropyron repens* usually only ten to eleven aerial leaves are borne on each main shoot, it follows that in apices dissected from relatively mature shoots, only a few of the more basal primordia are destined to develop to completion. The primordia still arising appear normal and in sectioned material seem to be initiated in the normal way by periclinal divisions in the 'dermatogen' and hypodermal layers, but they are fated to cease growth early.

Initiation of the inflorescence

In more mature material the apex appears more elongated and in place of the normal leaf primordia there are observed double ridges with the upper part of each pair often larger and more tongue-like when the apex is viewed in the plane of the leaves, Pl. 1 *u-x* and Pl. 2 *a* and *b*. The tongue-like structures are the spikelet buds, and the lip-like ridge below each is the primordium of the subtending leaf. Stages such as those shown in Pl. 1 *u-x* and Pl. 2 *a, b, e, f* and *g* leave no doubt as to this relationship.

The change over from the purely vegetative stage of the type shown in Pl. 1 *k* and *l* or *p* to inflorescence stages of type shown in Pl. 1 *v-x* must be extremely rapid, for it has not been possible to get many intermediate stages; the apex photographed in Pl. 1 *q* and *r* probably represents the change over and that in Pl. 1 *u*, where there are about five spikelet buds, shows one of the earliest stages of an undoubted inflorescence that was found.

At about the maturity of the inflorescence shown in Pl. 1 *u-x* the tip is still growing and further new leaf primordia and their axillary spikelet buds are continually being added, but now the buds develop so precociously that they and not the leaf primordia are the conspicuous feature; in fact, in dissected material it is often difficult to feel convinced that the primordia subtending the uppermost buds can be seen at all. Microtomed material, however, would suggest that they are always initiated (by the usual periclinal divisions in the dermatogen and hypodermal cells) even although their lateral extension may be localized and their development either be very slow or cease early. Even in sections, however, it is not at all certain that these later primordia are always initiated *before* their respective axillary buds!

As the season advances it becomes increasingly difficult to find apices which are either elongating prior to inflorescence initiation or have just commenced to produce spikelet buds. Finally, by about the third week in May, it is only possible to find young but definite inflorescences or obviously vegetative apices, i.e. stages with a morphology equivalent to about those of Pl. 2 *a* and *b* or Pl. 1 *f-i*. After observations over four years during the critical period in early May, the impression gained is that if a shoot has not formed the requisite number of leaves (and therefore attained the correct maturity) by the time the day-length reaches a certain value, it cannot initiate an inflorescence. What happens to an apex which has become rather long but is still not sufficiently advanced, is still unsolved, but occasionally apices like that shown in Pl. 1 *s* and *t* are found, suggesting regression from a long apex to a typically vegetative type.

At the time the inflorescence is being initiated at the main apex, the blind shoots become the conspicuous feature of the plants as seen in the field. These are growing rapidly in length but when dissected are found to contain very short apices, which remain of this type throughout the life of the shoots; a typical one is shown in Pl. 1 *y*. During dissections of blind shoots the young leaves always seem pliant and do not cut crisply, suggesting that they are suffering from lack of water—indeed the apices themselves and the one or two primordia only just produced give the same impression.

Inflorescence development

In the *Agropyron* material examined, the adult inflorescence usually bore about twelve to fourteen spikelets, though occasional individuals with up to twenty could be found. There is no obvious correlation between the number of spikelets developed and the time of appearance of the inflorescence, although observations on wheats suggest that a careful study might show that earlier spikes tend to carry more spikelets.

Apparently the first spikelet bud to grow out and hence be visible externally in dissected material, is not necessarily the one which is the lowest in the final mature inflorescence. This is suggested by the fact that stages like those of Pl. 2 *e* or *g* usually show one or two very small buds at the base of the inflorescence; since these are less well developed than the ones seen at the base in younger stages of the inflorescence (e.g. like those of Pl. 1 *u* or *v-x*) it seems certain that they have appeared externally later than those immediately higher up. This, however, does not mean that they were actually *initiated* in that sequence. In serial sections of material at the critical time when the apices are changing from the vegetative state to inflorescence production, it is possible to see the first stages of spikelet bud initiation long before there is any suggestion of their growing out, thus paralleling the condition found in purely vegetative shoots (Sharman, 1945 *b*). It would seem that, although the buds are initiated in strict basifugal succession, each commences its further development earlier in the history of the axis unit with which it is associated and perhaps carries out its development at a greater speed. Thus the buds would appear *externally* first somewhat above the extreme base of the inflorescence and the rest in succession both basipetally and basifugally from this region. Specific variations in the earliness at which the spikelet buds begin to grow out and in the amount by which each succeeding higher one grows faster than the one below, would account for the observed variations in inflorescence development in different grasses, ranging from those with completely basifugal to apparently completely basipetal spikelet development. The latter would be the result

of the original basifugal initiation being followed by very late development, perhaps also associated with a high growth rate in the upper buds.

Onset of spikelet differentiation

After about a dozen spikelet buds have grown out it seems that, although the tip of the axis is still producing crescentic leaf primordia, buds no longer appear precociously in their axils, Pl. 2 *c-d* and *i*. The leaves now being initiated are the future two glumes and the lower lemmas of the terminal spikelet, with the result that the length of the inflorescence is now determined. The complete continuity in the series of leaf primordia from vegetative leaves through the collar leaves subtending lateral spikelets to the glumes and lemmas of the terminal spikelet explains why the terminal spikelet always lies at right angles to the plane of insertion of the two rows of lateral spikelets, i.e. 'across the head' as the agriculturalist would say of a cereal spike.

Buds soon appear in the axils of the two lowest lemmas of the terminal spikelet (Pl. 2 *e, f*, and *g*) and thereafter new lemmas and their axillary floret buds are produced in succession, Pl. 2 *j, k* and *l*. Soon the stamens appear as three protuberances whose shape and general appearance strongly suggest that they are more in the nature of buds than leaves, Pl. 2 *k* and *l*. Although the point was not pursued, it seemed that the two dorsal stamens appear first and are placed diametrically opposite each other, so that when the third (anterior) one appears it is at right angles to their insertions, so that the three are not in a true, equally spaced, trimerous whorl. The palea, presumably the equivalent of a prophyll on the axis of the floret bud in the axil of the lemma, can usually be distinguished in dissected material when the stamens are fairly well formed (Pl. 2 *j, k* and *l*), but no attempt was made to determine when it is actually initiated.

Although not illustrated in the accompanying photographs, the mode of initiation of the carpel is similar to that of a normal (single) leaf primordium, except that the encircling growth seems a little slower. Perhaps this reduction is merely the first sign of a new internal economy which is also responsible for the slowing down and final cessation of the growth of the apex tip itself whilst it is being enclosed within the carpel and transformed into the single ovule.

Floret development is basifugal in each individual spikelet and is farthest advanced in the terminal spikelet. In each successively lower lateral spikelet it is less advanced, so that, for example, stamen development can be taking place in the upper spikelets before even the lemmas have appeared in the lower ones. This again reinforces the idea that the higher spikelets develop faster than those lower down the inflorescence.

DISCUSSION

Having presented a picture of the sequence of events in *Agropyron*, the salient features may be compared with those seen in other species, and some of the commoner 'anomalies' found amongst the grasses correlated with developmental morphology.

Apex morphology

The length of the apex varies from species to species, even within a single genus, but for any particular species it is usually fairly constant provided shoots of the same maturity and of equivalent vigour are compared. Since a number of points are associated with differences in length, it has been suggested (Sharman, 1942*a*) that grass apices can best

be considered in three groups (long, intermediate and short), although in reality, of course, there is a complete gradation of types. However, the use of three categories gives a convenient method for analysis.

The long type occurs in *Lolium multiflorum* Lam. (Pl. 3d), *Anthoxanthum odoratum* L. (Pl. 3e) and *Melica altissima* L. In the first two species the writer has seen apices, apparently still vegetative and without any suggestion of spikelet buds, bearing up to thirty leaf primordia; fifteen to twenty primordia are not at all uncommon. In this group there is much variation in the number from shoot to shoot and there seems to be a continuous lengthening of the apex and an associated piling up of young primordia from the seedling or axillary bud stage right until the onset of inflorescence initiation, with no very marked elongation just prior to the change over. Although the point has not yet been thoroughly investigated, judging by the number of adult leaves which reach maturity on the main axis, in at least *Lolium multiflorum* and *Anthoxanthum* many apparently normal primordia develop no farther than small collars subtending the spikelets or panicle branches in the inflorescence.

The intermediate type, where the apex bears five to ten primordia, is not sharply delimited from the long type and is by far the commonest, being found in most of the herbage grasses, for example in *Agropyron*, *Agrostis*, *Festuca*, *Holcus*, *Phleum*, *Phalaris* and *Lolium perenne* L. Although very vigorous shoots may have longer apices than normal, the limits for any particular species are more clearly defined than in the long type, especially in those species tending to have rather shorter apices. Pl. 3b and c show apices of *Glyceria fluitans* R.Br. and a species of *Agrostis* (probably *A. alba* var. *repens*). There is some increase in the number of primordia carried as the shoots approach the end of the vegetative phase, but the main elongation seems to occur only just prior to inflorescence initiation (Pl. 1p, q and r, u and v-x)—see also Evans and Grover (1940) and Weber (1938, 1939).

The short type of apex, bearing only one to perhaps three primordia is found in *Avena*, *Oryza*, *Saccharum*, *Secale*, *Sorghum*, *Triticum* and *Zea*,* and seems to be common in the cereal grasses. Typically it has a morphology similar to that of the *Agropyron* rhizome apex (Pl. 1a-c) and remains short throughout the whole of the vegetative phase, only elongating suddenly and rapidly at inflorescence initiation, when precocious axillary buds arise in the normal way. This late elongation is very sudden in a type like *Zea*, but in *Triticum* there is a tendency to elongation during the initiation of the last vegetative leaves.

The suggestion that short apices are characteristic of annuals and long ones of perennials is invalidated by the occurrence of short apices in *Phyllostachys* and *Saccharum* and of the intermediate type in *Poa annua* L., and the long type in *Lolium multiflorum*. Nor can the type of apex be correlated with a monocarpic or polycarpic habit since although most bamboos, at least of the genus *Phyllostachys*, die after flowering, this is not the case in *Saccharum* (Janaki-Ammal in letter, 24 November 1941). Again, although plants of *Poa annua* and *Lolium multiflorum* can be kept alive after flowering, they show a strong tendency to die out unless special care is taken.

* Noguchi (1929), investigating cereals of this type, is obviously in error in regarding the shoot apex of the caryopses and young seedlings as being young inflorescences. Even in the most precocious spring types, grown under the optimum conditions of day-length and temperature, the apices do not develop directly into inflorescences but all have to initiate a number of additional primordia destined to grow up into normal leaves.

Nor does there appear to be any connexion between the type of apex and the degree of tillering exhibited by the species. *Coix*, *Phyllostachys* and *Saccharum* all have short apices and yet they tiller as well as many of the common herbage grasses. Again, in a number of strains of maize with a pronounced tillering habit, the apices were indistinguishable from those of normal, almost non-tillering strains.

It has been suggested (Sharman, 1942*a*) that the clue to the length of the apex probably lies in the behaviour of the provascular strands. In *Dactylis* and *Melica*, Bugnon (1924) reported that the first provascular strands are initiated in the 'disk of insertion' of the primordium and develop upwards into the primordium and downwards in the axis to link up with those from more mature leaves: exactly the same situation is found in *Lolium multiflorum* (unpublished), whilst in *Zea* they first appear rather lower in the axis (Sharman, 1942*b*). Now, if they are initiated early and link up early in the history of the primordium, they will soon be able to tap 'food' supplies coming back from the older leaves and water supplies from roots growing out from lower nodes. This would presumably mean that the primordium would soon be able to grow rapidly and leave the immediate region of the apex, especially as this phase is mainly due to the 'vacuolating-and-dividing' type of growth (ripen meristem). On the other hand, when the initiation or linking up of these independent provascular systems is slow, there might easily be a piling up of primordia on the apex, especially if the main requirement is water rather than 'food'. So far, unfortunately, there does not appear to be any information on the relative times at which leaves in different species become linked with the main vascular system.

Shoot types. (a) Aerial shoot

Although it is still difficult to see any very exact plan underlying the types of shoots produced by different grass species, some of the variations have a number of points in common. In *Agropyron* there are the normal shoot, the blind shoot and the rhizome. At first it seemed possible that the blind shoot arises when the fate of the main axis to produce an inflorescence has been determined and when this apex is presumably drawing heavily on the main food or water supplies of the plant, but observations soon showed that the blind shoots commence elongation and are consequently distinguishable from the main shoot while the apex of the latter is still comparatively short and still producing primordia destined to develop into normal foliage leaves. The main axis only 'shoots', to use the term of the agriculturist, after the inflorescence has been initiated, which is some considerable time after the blind axes have begun to elevate.

Many of the blind shoots die during the summer, but when one does manage to survive, the buds in the axils of its leaves grow out and by multiple branching, produce tufts of short leafy shoots at each node (cf. the mop-habit described by Arber (1934) for a number of grasses).

Shoot types. (b) Subterranean

At first it was thought that the buds which grow out as rhizomes do so because they are situated underground, and that their leaves develop into scales instead of aerial leaves owing to the conditions of aeration, darkness, etc. under which they are developing. Although this may be partly true, it cannot be the whole of the explanation. When rhizomes are planted in soil in a receptacle kept in the dark, the shoots which emerge are

etiolated but the leaves are still differentiated into lamina and sheath. Again, if the soil is dug away from the side of an *Agropyron* plant so that in spring the rhizomes grow out directly into the light, they do not develop into aerial shoots but continue as rhizomes with green *elongated* internodes, bearing green scale leaves. They exhibit no negative geotropism and it is only later in the season that the ends commence to grow upwards and at the same time begin to bear the aerial type of leaves. These 'aerial rhizomes' and blind shoots link up well with the normal shoots of bamboos, which habitually produce vertical axes with elongated internodes and either scale leaves or leaves which are differentiated into large sheaths and reduced laminae, very reminiscent of the transitional leaves of *Agropyron*. In the bamboos it is obvious that the production of these shoots is not connected with inflorescence initiation. Later the development and multiple branching of the buds in the axils of the scale and transitional-like leaves on the main bamboo stem result in the tufts of shoots carrying typical foliage leaves; this state essentially parallels the pom-pom habit of old blind shoots in *Agropyron*.

If caryopses of *Agropyron* are germinated, the main apex produces only a blind shoot and never seems to develop into an inflorescence. The buds in the first two or perhaps three leaves grow downwards and give rhizomes, a habit which also seems to be found in bamboo seedlings (see Arber (1934) quoting Brandis (1899)). Thus we have types like *Agropyron*, the bamboos and possibly *Saccharum* where the seedling apex never develops into an inflorescence, in antithesis to such types as *Zea* and some spring strains of *Triticum* where, except perhaps under drastically altered conditions of day-length and temperature, tillering is extremely poor and the whole plant usually only produces a single shoot which ends in an inflorescence. In these types the only axillary buds to develop are the lateral spikelet buds and the floret buds of the terminal spikelet in the case of *Triticum*, and the panicle branches and the cobs in the case of *Zea*. In plants like this it is as though their whole course is pre-set and governed by a sort of 'physiological time switch' so that if the day-length and temperature are kept constant, the onset of flowering cannot be started until the appropriate number of leaves have been initiated; nor can it be delayed beyond this stage. Neither the continual removal of considerable portions of the photosynthetic area nor wide variations in the available nitrogen, phosphate, etc. will delay or accelerate flowering (Purvis (1934), Sharman (1942c)). Of course such treatments greatly alter the rate of initiation in terms of absolute time and so alter the date of flowering but they do not influence the number of leaves which are produced; they do not, in fact, alter the internal 'physiological timing'.

The apex and leaf types

Although there is considerable variation in the final appearance of the various types of leaves on the *Agropyron* shoot, a perusal of the figures will show that although there is a steady elongation and piling up of the young primordia just behind it, the apex tip itself maintains an unaltered appearance right until it is the end of the rachilla of the differentiating terminal spikelet, as in Pl. 2 *l* or Pl. 3 *a*. Nor during its history does there appear much internal difference in the construction of the extreme apex, either in architecture or even in the cytological appearance of the cells in vacuome fixed material. It seems certain that the apex tip itself has no say in the future development of any leaf primordium once it has been initiated, and that other factors determine whether any

particular one is to develop into a scale leaf, a foliage leaf, a collar at the base of a spikelet, a glume or a lemma.

Collar leaf and spikelet insertion

As is well known, in the inflorescence of *Lolium* the insertion of the spikelets on the rachis differs from that in *Agropyron* in that they are placed 'edgewise on' to the axis. Since the spikelets of *Lolium perenne* and *Lolium multiflorum* have only one glume which is on the outside of the spikelet, it might be thought that this is morphologically equivalent to the collar leaf of *Agropyron*. Examination of dissected material of young stages, however, shows that this is not the case and that the glume is truly borne on the spikelet axis and that a collar primordium can be seen subtending each of at least the lower spikelets. This accords with the observation that a collar leaf can sometimes be detected in mature inflorescences in this species. In this connexion it is interesting that in *Lolium temulentum* L. there is a small second glume on the side nearest the rachis in each of the lowest spikelets. Again, in '*Festuca loliacea*' Huds. which is almost certainly a collection of hybrids between *Festuca pratensis* Huds. and *F. arundinacea* Schreb. on the one hand and *Lolium perenne* and *L. multiflorum* on the other, a single clone will produce inflorescences ranging from ones as branched as *Festuca* to others which are almost completely *Lolium*-like spikes; in the latter the lower spikelets are arranged at an angle to the axis and have a small second glume on the side nearest the axis, whilst the upper spikelets are often arranged as in *Lolium* and only have a single glume which is situated on the outside. The spikelets with two glumes are very like the single spikelets found at the top of a normal *Festuca* panicle.

Leaf sequence

The fact that there is a continuous sequence of leaves up the whole of the main axis is particularly interesting in a grass like *Anthoxanthum* (and presumably also in *Agrostis*, *Alopecurus* and *Phleum*), where the inflorescence ends in a terminal spikelet containing a single terminal flower. The carpel is initiated in the same way as a normal leaf and thus in the terminal spikelet must represent the last leaf on the main axis, since it and the glumes, etc. continue the strict distichous continuity of the shoot.* Furthermore, after the initiation of the carpel, the apex tip becomes enclosed by the latter and transformed into the ovule, when the now single initial in the hypodermis becomes the megaspore mother cell. Little of a more terminal nature could surely be found!

Anomalies and their significance

When terminal spikelets of a number of *Agropyron* inflorescences are examined, about 5% are found to be anomalous. Variations may be seen ranging from a floret in the axil of what should be the upper or lower glume to a whole lateral spikelet subtended by the equivalent of the lower glume. Such anomalies would be expected when it is realized that the glumes of the terminal spikelet and the collars subtending each lateral spikelet are all initiated as leaf primordia and are all potentially capable of having buds in their axils.

Similarly, it is not surprising to find any of the buds of either a terminal or a lateral spikelet growing out into a miniature shoot of its own, as in cases of proliferation or

* In grasses with more than one flower in each spikelet (as, for instance, in *Agropyron*) these are borne laterally, developing at the end of the rachillae derived from the buds in the axils of the lemmas; the carpels arise on these as in *Anthoxanthum*.

so-called vivipary. Jenkin (1921) and Philipson (1934) show quite clearly the equivalence of the lemmas to normal foliage leaves by their occasional development into small leaves, which may be sterile or still bear florets in their axils.

In the inflorescence one would expect that the collars would occasionally develop rather more than usual. This does in fact happen (Pl. 4 *c*) and it is extremely easy to collect a series of inflorescences ranging from ones where the lowest spikelets are subtended by small bract-like structures up to examples with well-developed foliage leaves. In *Agropyron* this excessive growth is limited to the primordia of the lower part; those subtending the spikelets higher up only produce an occasional rather exaggerated collar. In *Triticum*, however, any of the lateral spikelets may be subtended by quite glume-like leaves. In *Hordeum*, Vavilov & Bukinich (1929) figure a variety where the lowest triplet of spikelets is subtended by a small leaf, but there does not seem to be any confirmation that this character is hereditary.

The occasional production of a bud leading to the development of an inflorescence in the axil of the topmost (or 'flag') leaf is not unexpected.* Examples of this have been seen in *Avena*, *Dactylis*, *Hordeum*, *Lolium* and *Secale*, and could doubtlessly be found in any grass. Although such supernumary inflorescences are regarded as anomalies in these types, in *Sorghum* (Panicoideae) and related genera each of the higher leaves on the shoot bears an axillary inflorescence. An extension of this is the normal occurrence of well-developed leaves in the inflorescence at the point where the panicle branches join the main axis, a type of habit common in *Panicum* and which again links up with the occasional over-development of the spikelet collars in the middle of wheat spikes, etc. as described above.

Agropyron inflorescences can sometimes be found with a pair of spikelets at each node, as in Pl. 4 *e, f* and *d* (mid-region). This condition may occur along most of the inflorescence or it may be confined to a single node. Often the two spikelets differ in size and whilst the larger is in the normal position, the plane of the glumes, etc. of the smaller may be almost at right angles to it (Pl. 4 *e* and *f*), suggesting that it is the morphological equivalent of a bud borne laterally on the axis of the larger spikelet. Inflorescences such as these duplicate the condition which is normal for *Elymus*, and the parallel is even more striking when it is realized that towards the top and base of many inflorescences of *Elymus* there are only single spikelets at each node. Furthermore, triple spikelets can occasionally be found in *Agropyron* (Pl. 4 *g*), whilst they are extremely common in *Elymus arenarius* L. and are the normal condition in *Hordeum*, where both from the adult appearance and their mode of development (Pl. 3 *g* and *h*) they suggest a central main bud bearing two laterals, a view which is supported by the fact that in some species (e.g. *H. bulbosum* L.) all three spikelets are raised on a small pedicel.

Mention should be made of *H. europaeum* All. which is sometimes classified as an *Elymus* (*E. europaeus* L.). In this plant sometimes only the two spikelets are developed at each node, hence its inclusion in the genus *Elymus*. On the other hand, a rudiment of a central spikelet or even a well-developed one may often be found, justifying inclusion in the genus *Hordeum*.

* Buds are not normally detectable externally in the axils of the last foliage leaves, but in microtomed material the early stages in their initiation may be found, associated in the normal way with the leaf primordia. Apparently the earliness with which the topmost internodes commence elongation causes the internal potential bud tissue to be pulled out vertically so that its growth is in some way accommodated without the formation of the usual up-pushing which would normally lead to the external appearance of a bud.

In branched headed barleys, any one of the three buds may grow out into a branch of its own (Sharman, 1943) giving a rather simple panicle. When this happens to more than one bud at the same level there is an approach to the more complex type of panicle typical of many of the grasses (for example, *Agrostis*, *Festuca*, *Poa*, etc.) where many branches arise at one level and themselves branch some distance from the main axis, giving shoots of tertiary, quaternary and higher orders. The nearest to a panicle which could be found in *Agropyron* is that shown in Pl. 4 *d* and *h* where a central bud has grown out into a short branch from between two simple spikelets which themselves presumably represent two buds lateral and secondary to the central one.

Simple panicles are common in *Lolium*, whilst in *Triticum* they are the typical normal inflorescence type of certain varieties of *T. turgidum*, where many of the lateral buds grow out into small heads of their own instead of each only giving a single spikelet. Such varieties only give branched heads when grown under conditions of relatively short day-length; under longer days, types resembling *Hordeum* and *Elymus* can be produced with the spikelets in threes or even pairs at the nodes (unpublished). Under still longer days, the heads develop like those of normal wheats with only a single spikelet at each node.

In all these branched forms, the buds which most frequently grow out or which usually do so most vigorously are those just above the extreme base rather than the basal ones themselves. This is doubtlessly the resultant of two opposite effects, the faster growth of each successively higher spikelet bud on the inflorescence and the basipetal onset of spikelet differentiation. Towards the top of the inflorescence, extra growth would presumably lead to the production of a many flowered spikelet but towards the base it would result in the appearance of a lateral branch resembling a small head.

In rye the spikelets normally only contain two flowers each, presumably as a result of an early cessation of the growth of the spikelet buds; under suitable conditions of short day-length and low temperature they can grow out into 'viviparous' shoots (Kostoff, 1940).

Forked inflorescences

A rather different type of anomaly is that presented by inflorescences which are Y-shaped and bear spikelets along the base and both arms. Such a spike is shown for *Agropyron* in Pl. 4 *a*, and the writer has seen similar ones in *Lolium*, *Phleum* and *Triticum*. That the abnormality is due to a true forking of the rachis and not to lateral branch formation from a spikelet bud, is clearly shown by the fact that below or at the point of bifurcation spikelets can often be found ranging from what may be described as 'Siamese twins' to double spikelets where two normal ones are closely inserted side by side at the same level.

Thus, except in the last case, the conditions observed as abnormalities in one species can always be found as the normal habit of some other species, well illustrating the way in which the grasses ring changes on often quite simple modifications in a common fundamental ground plan.

SUMMARY

1. Photographs of dissections of the shoot apex of *Agropyron repens* (L.) Beauv. are used to illustrate the morphological features of the apex of the rhizome, the main and 'blind' lateral shoots.
2. With practice, grass shoots may be dissected using a minimum of apparatus, and the apices can be examined and photographed whilst still alive.

3. The apex is difficult to photograph but this can be achieved more easily when it is given a preliminary soaking, is examined, etc. in moist air and is only illuminated as sparingly as possible by a cool beam of light.

4. A brief description is given of a number of features of the gross morphology of *Agropyron* plants because these do not seem to be generally known and are pertinent to the biology of the shoot apex.

5. Rhizomes and early aerial shoots possess relatively short apices, bearing only a few primordia. As the season advances the main apex of the aerial shoot becomes longer and bears more primordia, seen in a closer series of developmental stages. A further rapid elongation precedes the appearance (externally) of the spikelet buds which are axillary to primordia destined to cease growth extremely early.

6. At the distal end of the young inflorescence, the apex tip continues to add primordia and spikelet buds, but the final extent of the inflorescence is fixed when it initiates the primordia which develop into the two glumes and succeeding lemmas of the terminal spikelet. These last primordia complete a distichous sequence continuous from the scale leaves of the rhizome, through the transitional and aerial leaves of the shoot and the primordia subtending the lateral spikelets.

7. Onset of differentiation in the spikelets is in succession from the terminal to the lowest lateral; in any single spikelet the production of florets is basifugal.

8. The stamen primordia look like normal bud primordia and bear no resemblance whatever to leaf primordia. The carpel arises as a single normal leaf primordium and represents the last produced by each floret apex, before it itself becomes transformed into the ovule.

9. At least in the area worked, after the third week in May, no more apices change over to inflorescences.

10. Any buds (other than those in the axils of the transitional or the last rhizome scales) which grow out only produce elevated shoots (termed here 'blind' shoots) which possess very small apices growing slowly and apparently lacking adequate water supply.

11. In representative material of a given stage, the length of the shoot apex is characteristic of the species. The length apparently governs the behaviour just prior to the transformation into an inflorescence, but is little if at all connected with taxonomy, tillering capacity, rapidity of onset of reproduction or life span.

12. Certain aspects recorded for bamboos and sugar cane can be paralleled in *Agropyron* by the blind shoots, the behaviour of rhizomes developing in the light and the early stages in the seedlings.

13. A number of anomalies are described and interpreted in such terms as continued growth of collar primordia and alterations in the behaviour of the spikelet buds. It is shown that the anomalies of one grass species are frequently the normalities of others.

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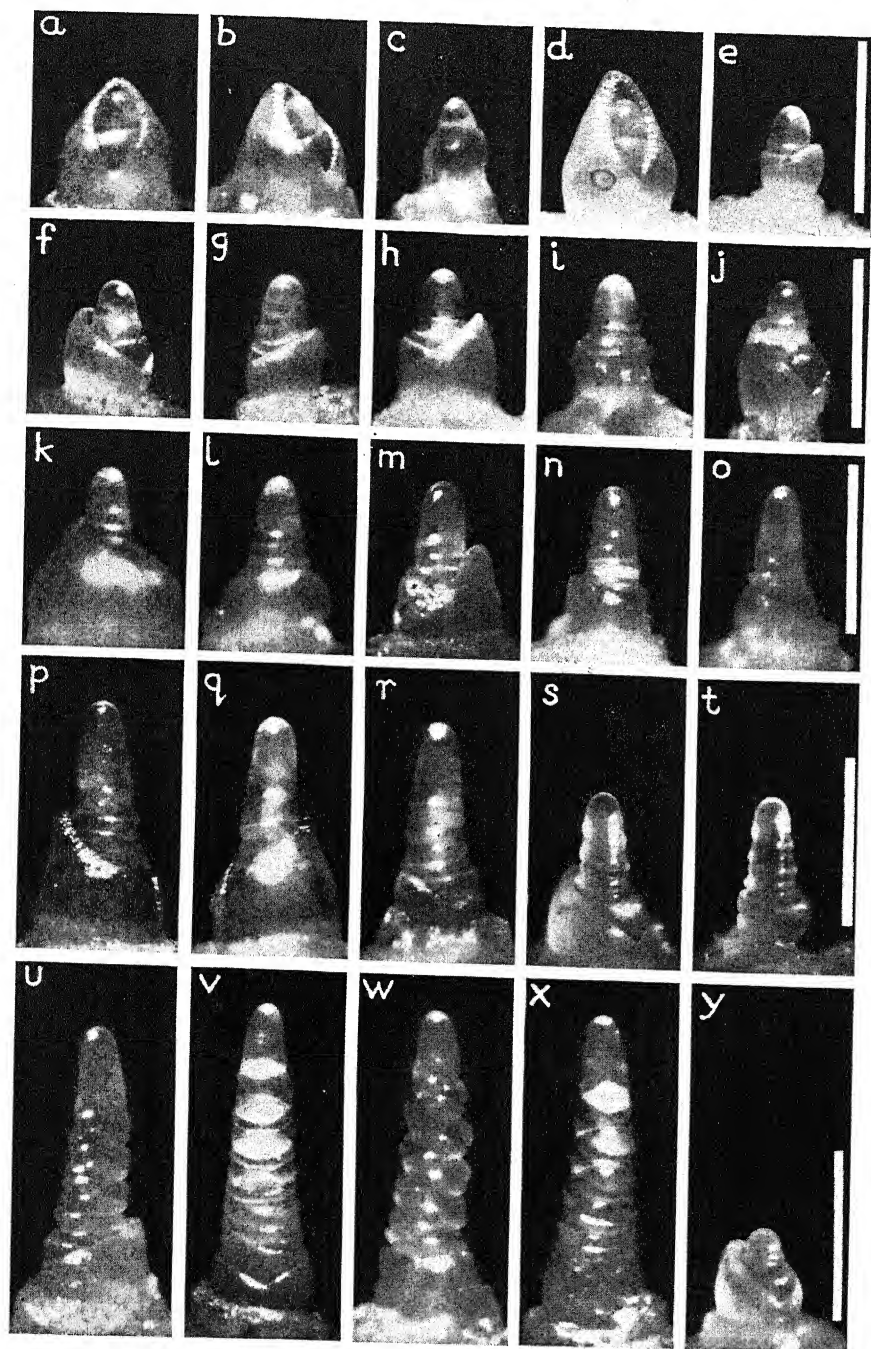
EXPLANATION OF PLATES 1-4

PLATE 1. *Agropyron repens*. Apices dissected from shoots of increasing maturity up to inflorescence initiation. *a*, *b*, two views of rhizome apex; *c*, the same apex with next leaf removed; *d-o*, apices from aerial vegetative shoots, *h* and *i* and *k* and *l*, each show an apex before and after removal of a primordium; *p*, late vegetative stage; *q* and *r*, an apex at change over from vegetative stage to inflorescence initiation; *s* and *t*, apex perhaps regressing after failure to initiate an inflorescence; *u*, early stage in inflorescence initiation; *v-x*, three views of young inflorescence, *y*, apex of blind shoot. Scale = 0.5 mm.

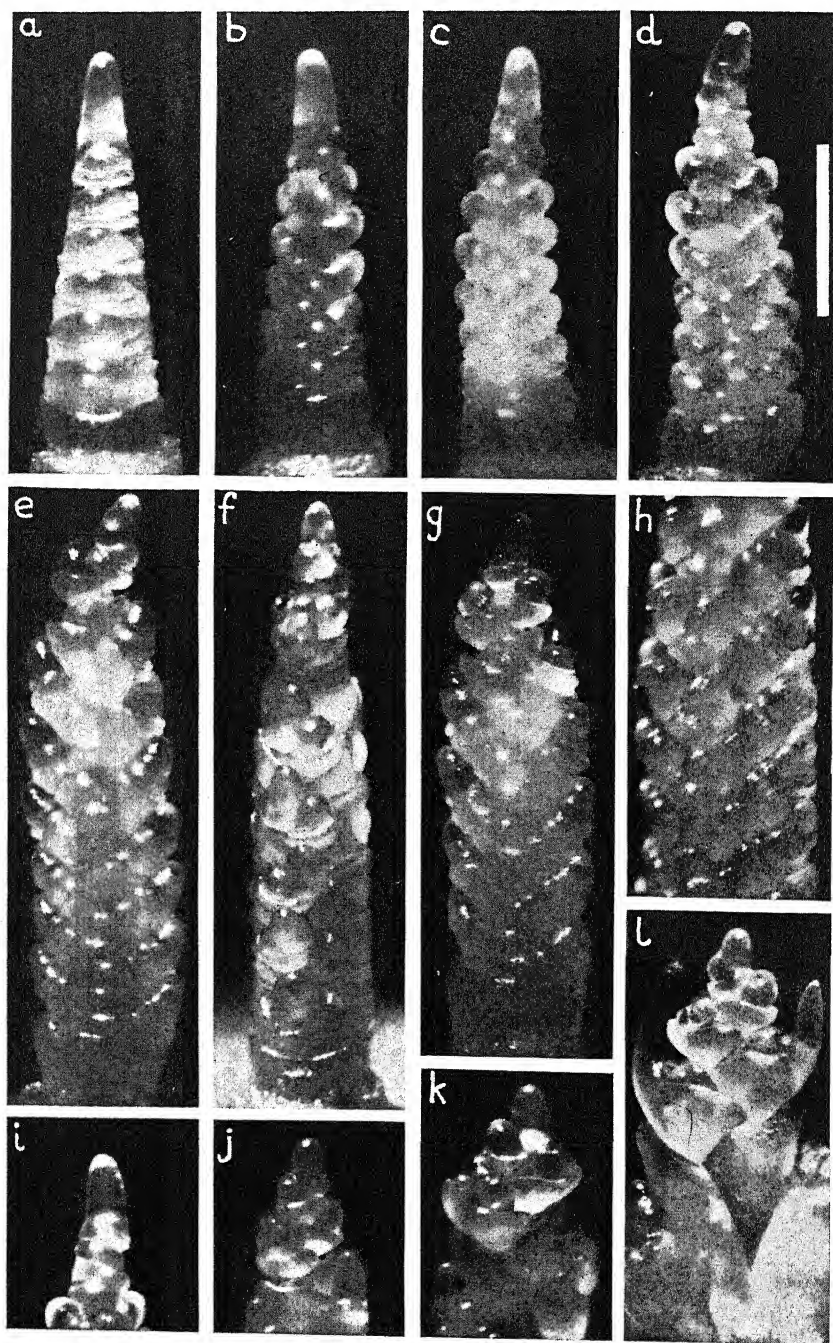
PLATE 2. *Agropyron repens*. Development of inflorescence. *a-c*, young inflorescences with spikelet buds and collar primordia (*a* and *b*, two views of same apex); *d-l*, later stages to show general development and also delimitation of inflorescence and differentiation of terminal spikelet (*e* and *f*, two views of same apex). The three stamen primordia are visible in lower flower of terminal spikelet in *k*. Scale in *d* = 0.5 mm.

PLATE 3. *a*, *Agropyron repens*, developing inflorescence (photographed in two parts). *b*, *Glyceria fluitans*, vegetative apex. *c*, *Agrostis (alba var. repens?)* vegetative apex. *d*, *Lolium multiflorum*, vegetative apex. *e*, *Anthoxanthum odoratum*, vegetative apex. *f*, *Anthoxanthum odoratum*, young inflorescence with apical spikelet just initiated the two stamen primordia. *g* and *h*, *Hordeum distichon*, two views of a young inflorescence, *g*, shows triplets of spikelet buds, each consisting of a large central one and two smaller laterals. Scale in *a* applies to all and = 0.5 mm.

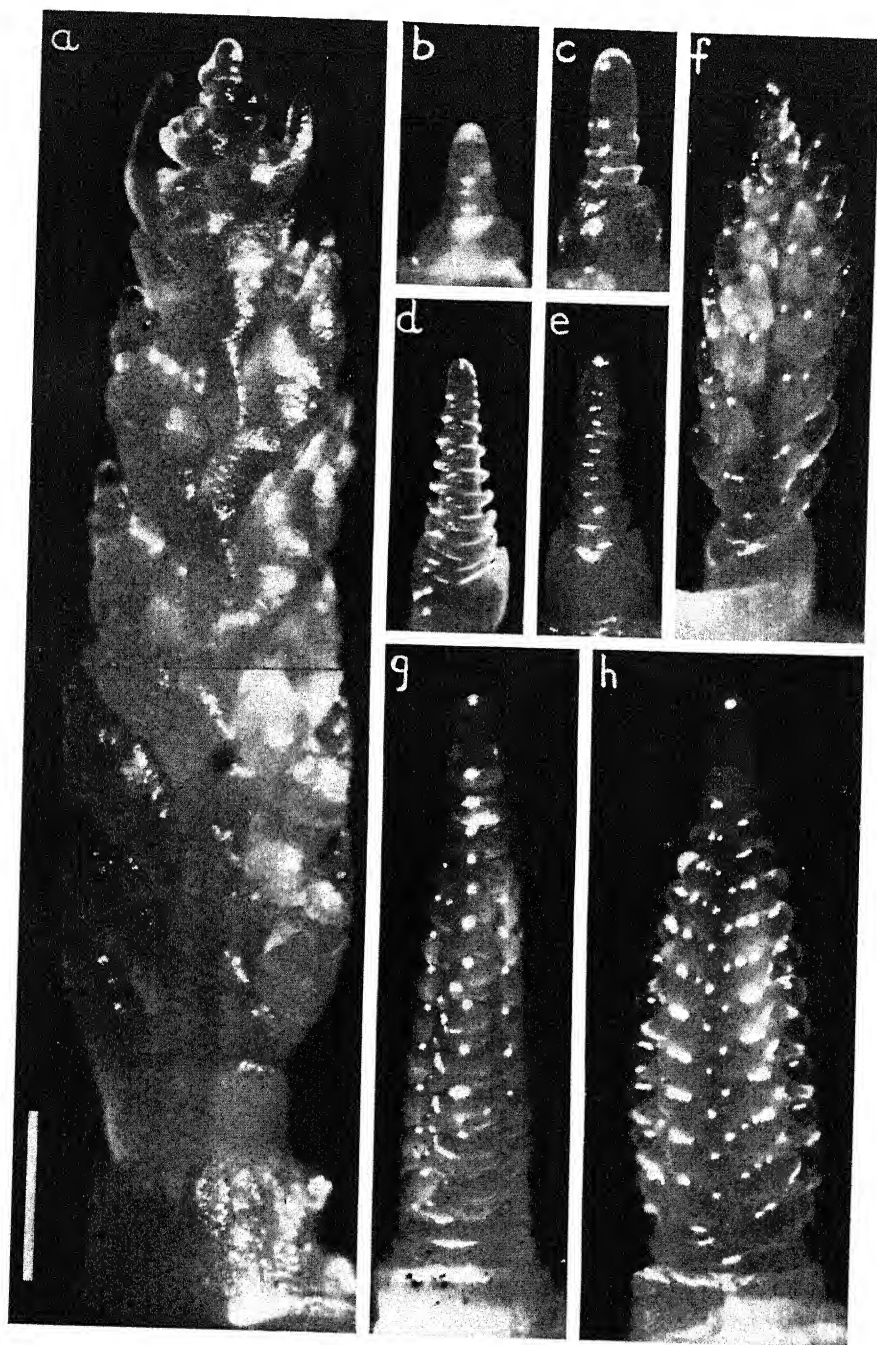
PLATE 4. *Agropyron repens*. *a*, forked inflorescence (see text); *b*, elevating blind shoots; *c*, bases of two inflorescences each with the lowest spikelet subtended by a miniature leaf; *d*, inflorescence bearing single and paired spikelets and a basal triplet whose central member has grown out into a small branch; *e* and *f*, paired spikelets; *g*, triplet of spikelets; *h*, another view of lowest node of *d*. *a*, slightly reduced, *b*, scale = 10 cm., the rest slightly enlarged.



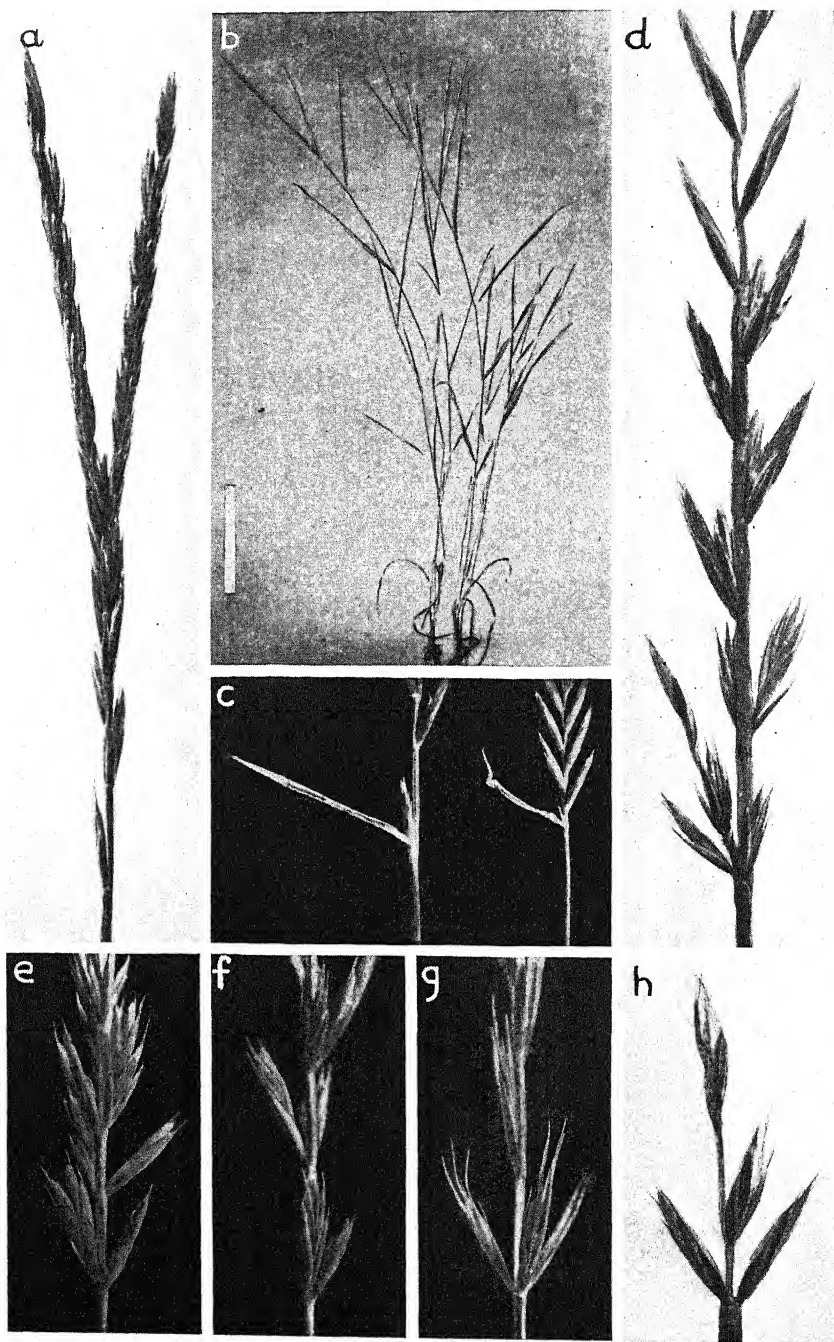
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OBSERVATIONS ON SOIL ALGAE

II. NOTES ON GROUPS OTHER THAN DIATOMS

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(With 6 figures in the text)

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A. INTRODUCTION

In a previous paper (Lund, 1945) a detailed account of the diatoms from sixty-six British soils was given. In fifty-four of these, more limited observations were made on the occurrence of the other algae, the results of which are here described. The methods of collection, examination and analysis are the same as those previously described (Lund, 1945, pp. 197-200, 202). Collections were not made during prolonged periods of drought or from soils that had been disturbed recently, in order, as far as possible, to eliminate these two factors as causes of the richness of the flora present. On the other hand, waterlogged soils or soils moistened other than by direct atmospheric precipitation were not examined, in order to exclude truly hydroterrestrial forms. It must be remembered, however, that there is no clear-cut margin between eu-terrestrial and hydroterrestrial habitats (Petersen, 1935, p. 2), since shaded soils may remain comparatively moist over long periods while hydroterrestrial habitats may dry up in periods of severe drought. Ground completely covered by vegetation was not examined. The aim was to study the normal flora of ordinary soils under reasonably favourable physical conditions.

Approximately the top 2 cm. were removed with a sterile knife or scalpel and placed in tobacco tins. Only the actual surface was examined in detail in all but one soil (see p. 44), but the complete slices of soil were used for the enriched samples (see p. 36)

so that any species living just below the surface would be included. Whenever possible the soils were examined on the day of collection, but the majority were examined on the day following and some 2-3 days afterwards.

In carrying out what are termed *direct observations*, the sample was removed by scraping portions of the surface of the soil slices with a sharpened edge of a triangular needle. Mounts were made on seven slides under $1\frac{1}{2} \times \frac{7}{8}$ in. cover-slips, as much soil being mixed with the sterile distilled water as possible without hindering microscopic observations. Using a $\times 10$ eyepiece and a $\frac{1}{6}$ in. objective, five longitudinal transects were made over each preparation. The algae present were noted and the unidentified specimens roughly drawn and measured.

The material from two of the preparations was run on to an agar plate (0.05 % Benecke solution in 2 % agar). A further sample of soil was placed in a Petri dish and moistened with 0.05 % Benecke solution. These last samples are hereafter described as 'enriched samples'. On top of this soil were placed a number of no. 1 cover-glasses sterilized by passing through a flame. The algae grew richly on the undersides of these cover-glasses which could be removed and examined under oil immersion, if necessary, in spite of any adherent lumps of soil or sand grains. Alternatively, they could be turned into drop cultures or placed in a moist chamber.

The numbering of the soils is that given in § G of Lund (1946). Some of the enriched samples and cultures (Lund, 1945, p. 199) were lost by enemy action before examination, and others before they were 12 months old, when the period of observation usually ended.

B. ECOLOGY

(1) *Results of the present investigation*

(i) *Productivity as established by direct observation*

Fig. 1 illustrates the relation between the richness of the flora on fifty-four soils and the readily available phosphates, nitrates, pH, base-deficiency and calcium carbonate.

The productivity histograms are shown separately for the different groups: Chlorophyceae, black; Myxophyceae, cross-hatched; and Xanthophyceae, *Chromulina* and *Euglena* plain. In the last group, C in the column indicates *Chromulina*, and M, *Euglena mutabilis*, a T, *Euglena* sp. and an X, Xanthophyceae. The productivity of the Chlorophyceae is given as greater or less than twenty, that of Myxophyceae as greater or less than ten, and *Chromulina*, *Euglena* and Xanthophyceae as present or absent. The different criteria were used because the productivity (Lund, 1945, p. 202, (a)) of Chlorophyceae ranged from 0 to 70, that of Myxophyceae from 0 to 30 and that of other groups from 0 to 10. The percentage of available phosphate in the soil (expressed as P_2O_5) is given as above or below 0.015 %, thus facilitating comparison with the results obtained for the diatoms (Lund, 1945, p. 203).

Chlorophyceae dominate the base-deficient soils and, in 16 of them, are the only class present. On the soils which are not base-deficient, the *Chlorophyceae*, though not so predominant, are equally abundant. The largest growths on such soils (apart from S8) occur when they are rich in available phosphates and, with the exception of S36, give a positive reaction for nitrates. The same relationship holds for the base-deficient soils less acid than pH 4.7, with the exception of S9, which was collected from the edge of a rabbit burrow, and though free from visible rabbit faeces may have contained urine. All the

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Fig. 1. Productivity in relation to chemical factors. For methods of compilation see Lund, 1945 fig. 1, and p. 36. Chl. Chlorophyceae; Fl. Chrysophyceae, C, Euglenineae (M, *Euglena mutabilis*; T, *Euglena* sp.) and Xanthophyceae X; Myx. Myxophyceae. +, present; -, absent.

Table 1. *Distribution of species relative to base-deficiency and pH (see p. 39)*

	Percentage of total occurrences		
	On base-deficient soils	On non-deficient soils	pH range
On the more calcareous soils:			
<i>Anabaena variabilis</i>	0	100	6.0-8.2
<i>Bumilleriopsis Peterseniana</i>	0	100	7.0-7.6
<i>Cylindrospermum muscicola</i>	0	100	6.0-7.4
<i>Cylindrospermum</i> spp. (IX)	0	100	6.4-8.2
<i>Dictyosphaerium minutum</i> (VII)	0	100	—
<i>Heterococcus Chodati</i> et spp.	0	100	7.2
<i>Phormidium autumnale</i>	0	100	6.4-7.1
<i>P. foveolarum</i>	0	100	6.0-8.0
<i>P. tenue</i>	0	100	6.0-7.5
<i>Tolypothrix tenuis</i> f. <i>terrestris</i>	0	100	7.1
<i>Tribonema bombycinum</i> (VII)	0	100	—
<i>Vaucheria hamata</i>	0	100	6.4-7.1
Mainly on the more calcareous soils:			
<i>Nostoc</i> spp. (I)	6	94	6.4-7.0
<i>Chlorella vulgaris</i> (VII)	7	93	—
<i>Microcoleus vaginatus</i>	8	92	6.4-8.2
<i>Heterothrix exilis</i>	10	90	5.5-7.5
<i>Vaucheria</i> spp. (II)	11	89	5.5-7.4
<i>Euglena</i> sp.	14	86	5.3-7.4
<i>Fernandinella alpina</i>	14	86	5.5-7.4
<i>Macrochloris dissecta</i>	17	83	5.4-7.0
<i>Phormidium</i> spp. (III)	23	77	5.5-7.4
Mainly on neutral to acid soils:			
<i>Stichococcus bacillaris</i> (IV)	30	70	5.1-7.4
<i>Hormidium mucosum</i>	40	60	4.7-6.7
<i>H. flaccidum</i> (V)	43	57	4.4-7.6
<i>Coccomyxa</i> spp.	46	54	4.4-7.4
<i>Cylindrocystis Brebissonii</i>	50	50	4.8-6.4
<i>Dactylococcus bicaudatus</i>	54	46	3.9-6.4
<i>Botrydiopsis anglica</i>	55	45	5.5-7.4
<i>Chlorococcum</i> spp. (VIII)	55	45	4.4-7.4
<i>Prasiola crispa</i> (VI)	55	45	4.8-8.0
Exclusively on acid soils:			
<i>Coccomyxa</i> A	100	0	3.7-4.6
<i>Coccomyxa</i> B	100	0	3.9-5.9
<i>Euglena mutabilis</i>	100	0	3.9-5.6
<i>Gloeocystis</i> sp.	100	0	3.7-4.6
<i>Mesotaenium violescens</i>	100	0	3.9-4.8
<i>Zygogonium ericetorum</i>	100	0	3.7-5.2

(I) *Nostoc* spp. include *N. commune*?, *N. minutum*, *N. muscorum* and *N. paludosum*.

(II) *Vaucheria* spp. include *V. geninata*, *V. sessilis* and *V. terrestris*.

(III) *Phormidium* spp. include *P. inundatum* and *P. uncinatum*.

(IV) *Stichococcus bacillaris*. The free-living forms may belong to various varieties similar to those forming lichen gonidia (Brand, 1913; Raths, 1938; Chodat, 1928), but no attempt has been made here to separate them.

(V) Including *H. nitens* (Menegh.) Klebs.

(VI) Only the *Hormidium* stage was observed.

(VII) Only observed in enriched samples and cultures.

(VIII) Mainly *C. humicolum* Naeg. (see Fritsch & John, 1942, pp. 375-7).

(IX) *Cylindrospermum* spp. include *C. alatosporum*, *C. licheniforme*, *C. stagnale* and *C. minutissimum*.

enriched samples from one base-deficient soil. This soil (S49) consisted of a small thin patch of acid glacial drift lying on limestone and surrounded by limestone rocks, so that the material may have been derived from the surrounding ground. *Microcoleus* and *Nostoc* may be considered as being calcicolous.

Chlorella vulgaris is so difficult to identify definitely by direct observation that all the records refer to enriched samples or cultures. It is, however, predominantly found on soils not deficient in bases.

Species confined to such soils included ten Myxophyceae, three Xanthophyceae and two Chlorophyceae, *Dictyosphaerium minutum* (only seen in enriched samples and cultures), and *Vaucheria hamata* (a.) shown in the first section of Table 1).

(2) *Discussion of results in relation to previous investigations*

It must be remembered that since only some of the species were identified, a number of those recorded by Fritsch & John (1942) may have been present.

(i) *pH and calcium carbonate*

My results are in general agreement with those of John (1942) who concluded that Myxophyceae and most Xanthophyceae are calcicolous and certain Chlorophyceae characteristic of acid non-calcareous soils (cf. Petersen, 1915). However, only four of her soils (nos. 21-4) are likely to be deficient in bases, her estimations of pH, like mine, being carried out colorimetrically. She includes two non-calcareous soils of pH 6.6 (nos. 18, 19) as acidic, but for practical purposes these are neutral and even her soil no. 20, pH 6.2, is unlikely to be base-deficient since it contains 0.13 % CaCO_3 . Her soils are therefore preponderantly neutral or alkaline and would not be base-deficient. The three definitely acidic and almost certainly base-deficient soils (nos. 22-4) contain no Myxophyceae, only one diatom and two Xanthophyceae, *Pleurochloris acidophila*, characteristic of acid soils, and *Botrydiopsis anglica*. On the other hand, there were twelve, thirteen and twelve Chlorophyceae present respectively on these soils. *B. anglica*, in the present survey, was rather more common on acid, base-deficient soils than on those which are not. Two of John's acid soils belong to a series of five from a grass heath which show very clearly the disappearance of Myxophyceae with decreasing alkalinity and absence of CaCO_3 . Esmarch's (1914) results for Myxophyceae are very striking. None occurred in thirty-five moorland soils and only two species in three out of thirty-seven sandy heath soils. The dominance of *Sphagnum* or *Calluna* on all these soils indicates clearly that they were base-deficient. Five species occurred in five out of forty woodland soils rich in humus. Though there are no vegetational details, these soils too were probably base-deficient. On the other hand, thirty-five out of thirty-seven loam and twenty-two out of twenty-three cultivated marsh soils contained a variety of species. Myxophyceae were of rare occurrence in the mainly acidic and probably base-deficient soils from Hammer Bakker examined by Petersen (1932a), while Chlorophyceae were predominant. Similarly, they were more frequent on the more fertile and less acid of the soils examined by Fenton (1943).

Euglena mutabilis occurs on all three of John's acid soils although it is not confined to the non-calcareous soils as in my survey. This species is common in highly acid waters (Lund, 1938, p. 273; 1942, pp. 254, 273*) though Lackey (1938) records it from waters of pH 2.9 and 7.3. Despite these exceptions, there can be no doubt that its main development is in highly acid and base-deficient soils and muds (cf. Fritsch & John, 1942, p. 394).

Zygonium ericetorum and *Mesotaenium violescens* are well known from acid heath and

* Also since found in a number of similar localities.

moorland soils (e.g. Fritsch, 1922*a*; Petersen, 1915, 1932*a*). The former often colours the surface of such soils. Petersen (1935) regards this species as hydroterrestrial.

Dactylococcus bicaudatus is recorded as characteristic of neutral to alkaline ground by Petersen (1915) but as mainly occurring on non-calcareous soils by Fritsch & John (1942), as was the case in the present survey.

Cylindrocystis Brebissonii (incl. var. *minor*) is recorded by Petersen (1915) and John (1942) on acid and neutral to alkaline soils but, like John, I found it to attain its maximum development on the former.

Nostoc muscorum is stated (Walp & Shopbach, 1942) to grow satisfactorily at pH 5, though pH 3.5 is lethal and an alkaline medium is slightly better than an acid one. In nature it does not appear to grow satisfactorily on acid, base-deficient soils, though it is not one of the commoner soil species.

Bristol (1920, see table III) gives no pH or carbonate data. Many of my samples come from the same regions as hers but it is impossible to compare our results, particularly as they refer mainly to cultivated land whose treatment or lack of it leads to very variable conditions in one and the same area. Her one peaty soil (no. 48) which comes from a strongly acidic and base-deficient area familiar to me, in culture, produced only Chlorophyceae. The six Wiltshire soils (nos. 49-54) on the other hand, which, from their location, were probably calcareous, produced more species of Myxophyceae than Chlorophyceae (or Bacillariophyceae). Smith & Ellis (1943) give a list of algae found in culture of three soils with pH 5.1-7.2. Several are not true soil algae but species of more or less wet rocks (e.g. *Gloeocapsa*, *Chroococcus*), plankton (e.g. *Microcystis aeruginosa*) or aerial habitats (e.g. *Protococcus viridis* = *Pleurococcus Naegeli*), while many widespread soil algae are not recorded, including all the diatoms. Taking into account only the probable soil algae, the soil of pH 5.1 produced no Myxophyceae and six Chlorophyceae, while that of pH 6.5 produced three and of pH 7.2, sixteen Myxophyceae; both the latter produced no Chlorophyceae.

Féher (1936*a*), on the basis of cultures, concludes that pH is of no significance, but that soil moisture is the most important factor. Thus he gives the following pH ranges for algae here recorded: *Cylindrospermum muscicola*, 7.11-4.64; *Anabaena variabilis*, 7.11-4.22; and *Mesotaenium violescens*, 7.16-4.99. While there can be no doubt as to the great importance of soil moisture, these wide pH ranges are at variance with my results and those of John (1942), Fritsch (1922*a*) and Fritsch & John (1942), and are probably due to the use of large samples including surface and subsurface soil for culture. Under these circumstances, occasional cells and spores of algae, though not able to multiply actively in nature, may be present and find the altered pH and calcium carbonate content of the culture favourable for development. This criticism gains added support from the occurrence in the cultures of several species which are not true soil forms (e.g. *Gloeocapsa* spp., *Bacillaria paradoxa*, *Pleurococcus Naegeli*, *Gloeotila protogenita*). In addition, the solutions and methods employed may have favoured non-terrestrial species. Though he cultured thirty samples of European woodland soils between latitudes 46 and 70°, many well-known and even ubiquitous soil algae are not recorded (e.g. *Hantzschia amphioxus*, *Navicula pseudatomus*, *N. mutica*, *Hormidium flaccidum*, *H. nitens*, *Prasiola crispa*, *Phormidium autumnale*, *P. foveolarum*, *P. tenue*, *Heterothrix exilis*). The same criticisms apply to another paper (Féher, 1936*b*), where 300-400 g. of soil were used for each culture, as well as to the joint paper with Killian (1939), in which, among the algae growing in cultures of desert soils, *Ulothrix zonata*, *Microcystis flos-aquae* and *Anabaena*

flos-aquae were described. In still another joint paper with Frank (1936) the cultures include such aquatic species as *Eucapsis alpina*, *Scenedesmus obliquus*, *Tetraspora lubrica*, *Dictyosphaerium Ehrenbergianum* and *Chromulina Rosanoffii*. Similar criticisms apply in part to Gistl's papers (1931-2; 1933).

(ii) *Nutrients*

Petersen (1935) states that, other things being similar, the content of nutrients in a soil determines the number of algae present, manured soils having the richest flora. Similar views are held by Bristol Roach (1927*b*) and Gistl (1933), as a result of the examination of untreated and variously fertilized plots. In so far as the Myxophyceae and Bacillariophyceae are concerned, my results largely confirm this but, as shown earlier, this does not hold for the Chlorophyceae, in particular for those characteristic of highly acid soils deficient in bases. The addition of solid inorganic fertilisers to the soil surface commonly leads to large macroscopically visible growths of green algae and the successful use of culture solutions for the study of soil algae is additional evidence for the stimulating effects of inorganic fertilizers.

It is known that diverse algae can grow in solutions containing organic nutrients and some in complete darkness. Little is, however, known about the relation of the algal flora to the various inorganic nutrients or of the effect of organic compounds. The latter have been thought to be of importance in relation to the occurrence of algae in the lower layers of the soil into which no light penetrates. Petersen (1932, 1935; cf. Esmarch, 1914) has brought forward strong evidence for the view that such algae are merely specimens carried down by the action of natural agencies and earthworms and that they do not multiply to any appreciable extent after burial. This is also the view of Fritsch (1936) and it is likely that it is only in the top few millimetres, at the most, that any appreciable sub-surface growth occurs (cf. also John, 1942). The work of Bristol Roach (1926, 1927*a*, 1928) is doubtful evidence for the growth of algae in darkness in the soil. The principal species studied (*Scenedesmus costulatus* var. *chlorelloides*) does not appear to be a typical soil alga since it has not been recorded by later investigators of a wide variety of soil habitats.* The sugars used are not known to be an appreciable part of the soil organic matter. Stokes (1940, *a*, *b*) found that, in the absence or presence of light, addition of organic matter inhibited partially or completely the growth of algae while the substances concerned were being broken down by bacteria and actinomycetes. He doubts the importance of heterotrophic nutrition in the development of soil algae and points out that the many other micro-organisms in the soil are better able to utilize organic compounds than algae. In the present survey there was no relation between the total content of organic matter and the richness of the algal flora. Moreover, my observations (cf. p. 45) indicate that Chlorophyceae grow on the surface.

Gistl (1931-2, 1933) has brought forward evidence to show that the various cations and groups of cations present are important in controlling the type of flora. He has paid special attention to sulphates and thiocyanates. He found (1933) unicellular Chlorophyceae and Xanthophyceae dominant in unfertilized soil and that treated with superphosphate (pH 5.5); filamentous Chlorophyceae and Xanthophyceae in that fully fertilized (pH 7.2); Myxophyceae in that treated with kainit and ammonium sulphate (pH 5.6) and unicellular Chlorophyceae and Xanthophyceae in that treated with superphosphate and ammonium sulphate (pH 5.6). The dominance of Myxophyceae in a soil of pH 5.6 is

* Except doubtfully by Skinner, C. E. & Gardner, C. G. (1930).

remarkable. A considerable number of more or less aquatic algae occurred in these cultures, as well as many true soil species.

De's (1939) proof that certain Myxophyceae, isolated from rice fields, fix atmospheric nitrogen has settled a long-standing controversy (see Petersen, 1935, pp. 118-22). Two of the species tested are common in British and other European soils, namely, *Anabaena variabilis* and *Phormidium foveolarum*. A variety of the former (var. *ellipsospora* Fritsch) assimilated elementary nitrogen when grown in nitrogen-free solution, while the latter did not. In the present survey both species occurred in soils which were not deficient in bases, usually rich in available phosphates and containing nitrates. *Anabaena variabilis* occurred in an enriched sample from a soil (S41) not originally containing nitrates, but was not present in large enough numbers to be observed by direct observation. Otherwise these two species were absent from soils not containing nitrates. Fenton's (1943, p. 411) Seafeld plot produced a rich growth of Myxophyceae from an area previously manured by cow dung while none arose from an unmanured area in the same plot. Bortels (1940, cf. Beijerinck, 1901), who studied nitrogen fixation by *Anabaena* and *Nostoc*, found that only these genera and *Cylindrospermum* arose in soil cultures containing no nitrogen. Fixation was slow in the absence of traces of molybdenum (also, to a lesser extent, of wolfram and vanadium). Stokes (1940*b*) similarly established nitrogen fixation in *Nostoc muscorum*. De (1939) showed that in the presence of nitrates growth was still good though nitrogen fixation was inhibited. It is, therefore, very doubtful if nitrogen fixation was of importance in the soils examined by me.

Fenton (1943) considers that the Myxophyceae phase, as observed by him in cultures, represents an ecological (or agricultural) climax, being correlated, among other factors, with soil fertility. He did not make any direct observations on the soils and his results may be explained in other ways. A Myxophycean 'climax' generally occurs in cultures or in soil samples kept moist in the laboratory over long periods provided that the original sample is not deficient in bases or highly acid (cf. John, 1942).^{*} Beijerinck (1901, cf. Bortels, 1940) found that Nostocaceae tended to predominate in soil samples treated with nitrogen-free solutions. It is, therefore, possible that the dominance of Myxophyceae in old cultures is connected with the reduction of the available nitrogen which may then be largely in the form of unavailable compounds or have been lost by denitrification processes. Clearly, it is desirable that the chemical changes occurring in soils maintained in cultural solutions, or kept continually moist in the laboratory, should be followed in conjunction with observations on the changes in the algal population.

(3) Seasonal succession and micro-stratification

Succession has been followed over a period of five years in a garden soil kept free of weeds, although in certain years (1940-2) only scattered observations were made. There was no seasonal succession of species such as is general in aquatic habitats. As with the diatoms (Lund, 1945, p. 208) the variations in numbers seem to be largely due to changes in the weather conditions (light, drought, frost and snow), February being a particularly unfavourable month.[†]

No detailed observations were made on micro-stratification (Fritsch, 1936, p. 20;

^{*} Mr Raeburn records the same feature; private communication.

[†] A table showing the detailed changes has been deposited in the library of the Freshwater Biological Association, Wray Castle, Ambleside, England.

John, 1942, p. 342), but the removal of the top millimetre of soil, on a few occasions when macroscopic growths were present, resulted in a great decrease in numbers as shown by the absence of a visible film of algae. The general paucity of Xanthophyceae may, however, be due to their being mainly subsurface forms (cf. John, 1942, p. 344).

C. TAXONOMY

Notes on some of the more important species: Only a part of the flora could be identified in the time at my disposal. The number of occurrences listed for each species refer to direct observation, agar cultures and enriched samples. For ecological relationships see B (1) and (2). The number of soils on which it occurred is given, in each case, in brackets after the specific name. The actual soil numbers (see Lund, 1946, p. 106) are given when a species occurred on a few soils of a particular type (e.g. highly acid).

(1) *Myxophyceae*

(1) *Anabaena variabilis* Kütz. (11). Never abundant and confined to soils not deficient in bases, usually accompanying the following species. World-wide distribution on soil (Petersen, 1935; Phillipson, 1935).

(2) *Cylindrospermum muscicola* Kütz. (9). Absent from base-deficient soils and very abundant on S1, 5, 11 and 30. Well known from soils (Petersen, 1935).

(3) *Cylindrospermum licheniforme* (Bory) Kütz. (S 30, 31, 43), Fig. 2 a-c. In the germination of the spores a zigzag split first appears in the outer membrane near one end. The contents enlarge and protrude through this split, the outer part of the membrane being left attached to the apex of the resulting filament produced (Fig. 2 c). The main body of the spore thus comes to have a dentate collar at the open end (Fig. 2 b, c). The basal cell of the germling remains in the spore and develops into a heterocyst. Recorded as common on soil by Petersen (1935; cf. Bristol, 1920).

(4) *Cylindrospermum minutissimum* Collins (S5, 44).

(5) *Cylindrospermum stagnale* (Kütz.) Bornet (S42). Recorded from an oak wood by Fritsch & John (1942). Petersen (1935) considers it as hydrophytic or hydroterrestrial.

(6) *Cylindrospermum alatosporum* Fritsch (S42). Recorded from soil by Fritsch & John (1942). Also known from the marginal mud of ponds (Lund, 1942). All these species of *Cylindrospermum* occurred on soils which were not deficient in bases.

(7) *Microcoleus vaginatus* (Vauch.) Gom. (13). One of the soils was base-deficient. World-wide distribution (Petersen, 1935).

(8) *Nostoc commune* Vauch. (S30, 31, 43). World-wide distribution (Petersen, 1935; Bristol, 1920).

(9) *Nostoc muscorum* Kütz. (S29, 31, 36, 42, 43). Known from British (Bristol, 1920; Bristol Roach, 1927b) and Australian (Phillipson, 1935) soils.

(10) *Nostoc minutum* Desmaz. (S41, 2). Recorded by Bristol (1920).

(11) *Nostoc paludosum* Kütz. (S30, 41, 43). Recorded from Britain (Fritsch & John, 1942) and Australia, Phillipson (1935).

The species of *Nostoc* were most common on soils which were not base-deficient but were found by direct observation only on S31 and 47 and then only as microscopic unidentifiable colonies. Yet *Nostoc* appeared in enriched samples and cultures from fifteen soils, so that spores, at least, must have been present (cf. also Bristol, 1919, 1920;

Bristol Roach 1927*b*; and Fritsch & John 1942). A search for macroscopic growths on bare ground over a wide area of midland and northern England and Scotland and Wales afforded scanty results. The only growths found were in a sand dune slack (once), on paths (four times) and grassland (twice). Species were, however, common amid tufts of mosses and liverworts. It would appear that *Nostoc* spp. are not characteristic of bare soil, although

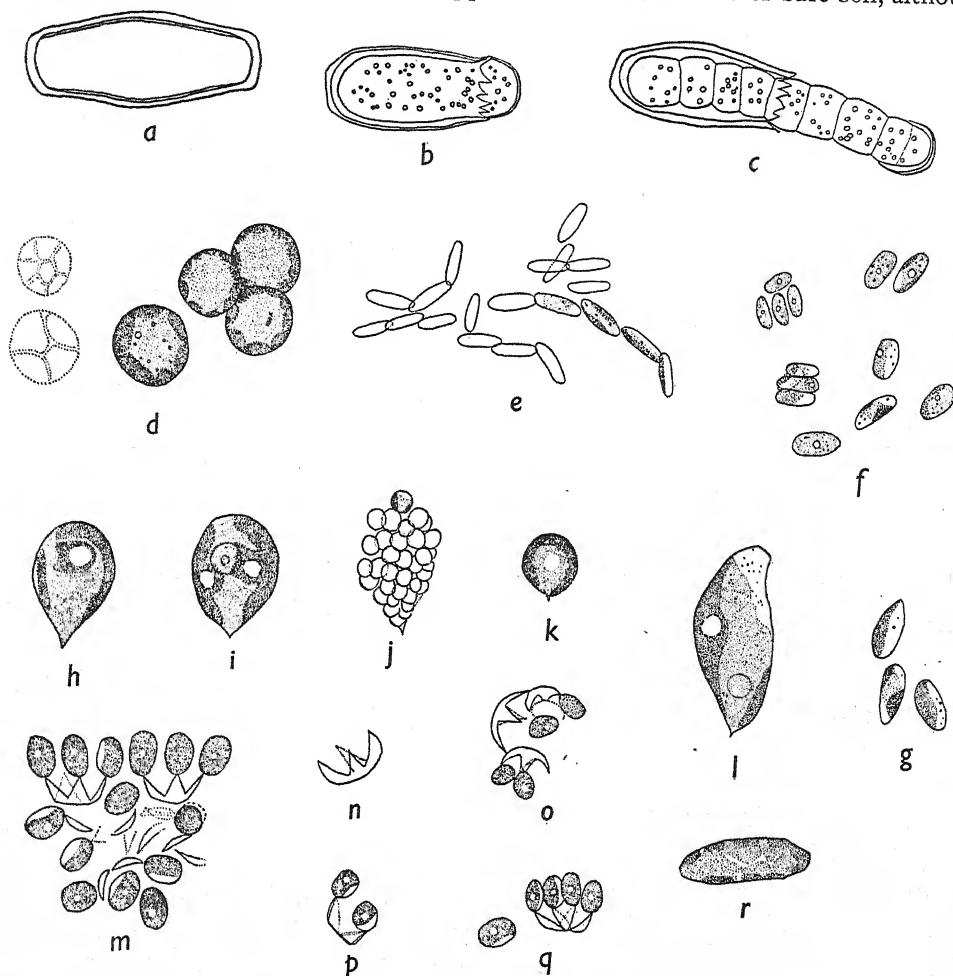


Fig. 2a-c, *Cylandrospermum licheniforme* (Bory) Kütz. a, spore; b-c, germination; d, *Muriella*, left, outline of chloroplasts as seen from above; e, *Coccomyxa* A; f, *Coccomyxa* B; g, *Coccomyxa* sp., James (1935, p. 523); h-l, *Characium pyriforme* n.sp.; m-q, *Dictyosphaerium minutum* Petersen; r, *Bumilleriopsis Peterseniana* Visch. & Pascher. a-e, g, m-r, $\times 1000$; f, h, l, $\times 750$.

isolated cells and spores must frequently be present. The spores are known to be very resistant (cf. Bristol, 1919). The large size of the adult growths perhaps gives an exaggerated idea of their frequency. Like other Myxophyceae, *Nostoc* spp. usually appear late in cultures or on soil kept moist in the laboratory, sometimes after a year or more (cf. John, 1942, pp. 346-7).

(12) *Phormidium inundatum* Kütz. (S46).

(13) *Phormidium autumnale* (Ag.) Gom. (15).

(14) *Phormidium foveolarum* Gom. (incl. var. *major* Elenkin) (14).

(15) *Phormidium tenue* (Menegh.) Gom. (12).

The last three species were found exclusively on soils which were not base-deficient. A few *Phormidia* occurred on base-deficient soils and thirteen unidentified species on other soils but in no case on a soil more acid than pH 5.5.

Direct observation always revealed only isolated trichomes, though these were sometimes common. When plated out on agar or kept moist in enriched samples, the typical papery strata arose. Prolonged access to moisture or periods of complete saturation with water may be necessary to produce the characteristic strata, since these are commonly found on surfaces which are very wet for longer or shorter periods, such as soils saturated with water (near drains and ditches, etc.) and wet rocks.

Phormidium autumnale, *P. foveolarum* and *P. tenue* have a world-wide distribution and are well known from British soils.

(16) *Tolypothrix tenuis* Kütz. f. *terrestris* Boye Pet. (S2, 41, 55, 56). On soils not deficient in bases. Frequent on S55 which was strongly calcareous (cf. Fritsch & John, 1942, p. 394).

(2) *Chlorophyceae*

(17) *Ankistrodesmus falcatus* (Corda) Ralfs f. *terrestris* Bristol (1920, pp. 49, 74). On S57, some two miles from Bristol's locality. Judging by Bristol's description and my specimens it is an ecotype rather than a form and Phillipson (1935) records the species from an Australian soil.

(18) *Characium pyriforme* n.sp., Fig. 2h-l (? *C. Naegelii* A.Br. sensu Bristol). The mature cells (up to 34μ l. and 13μ br.) are usually broadly pear-shaped (Fig. 2h, i), there being an oval body passing abruptly into a short pointed stalk without a basal disk. Occasionally, elongated and irregularly ellipsoid cells occur (Fig. 2l). The single parietal chloroplast covers a large part of the wall and contains one or, rarely, two pyrenoids. This latter state may be prior to division. There is one nucleus. The only method of reproduction observed was by numerous spherical aplanospores (Fig. 2j). The minute stalk is not visible until the cell has enlarged to at least twice its original size (Fig. 2k) and is free from the membrane of the parent cell. Zoospores are no doubt also formed since, when mature cells are placed in hanging drop cultures, daughter cells often occur separately at considerable distances from the now empty cells, after a day or so, congregating on the side nearest to the light source.

On agar plates (S13 and 41). In the delicate stalk it resembles *Stylosphaeridium* Geitler (Pascher, 1927, p. 482 et seq.), an epiphyte on plankton algae, but contractile vacuoles are absent. Bristol Roach (1927b) described a similar form from soil at Rothamsted as ? *Characium Naegelii* A.Br. This also showed a tendency to unilateral distortion of some of the larger cells and had a minute stalk about 2μ long, which was sometimes expanded basally to form a minute attaching disk. *C. terrestris* Kanthamna (1940), from a culture of an Indian soil, produces autospores but differs in the larger stalk with a definite attaching disk and the multinucleate cells.

Characium Sieboldii A.Br., recorded by Gistl (1931-2), is probably not a soil alga (cf. p. 45). *Chlamydomonas* spp. are the subject of a separate paper.

(19) *Chlorella botryoides* Boye Pet. 1932, pp. 36-7 (1). Recorded by James (1935, p. 528).

(20) *Chlorella vulgaris* Beyer (14). It is generally impossible to distinguish this species,

by direct observation, from other spherical green cells so commonly present. The unnamed variety described by Petersen (1932a, p. 36) occurred on S36.

(21) *Chlorococcum* spp. (23). Fritsch & John (1942, pp. 374-7) have shown that at least two species occur on soil. The various types were not studied but most of the specimens appeared to belong to *C. humicolum* Naeg. Probably present on a greater number of soils than those for which it is recorded. The isolated cells are often indistinguishable as such by direct observation and a number of cultures in which it may have occurred were destroyed by enemy action.

Coccomyxa Schmidle. In order to distinguish species of this genus cultural work is generally necessary (Jaag, 1933) and, in the absence of this, most of the specimens have not been named.

(22) *Coccomyxa dispar* Schmidle (1). A common aerial alga (cf. Fritsch & John, 1942).

(23) *Coccomyxa* sp. James, 1935, p. 523; cf. Bristol, 1920, p. 73. Fig. 2g (13). Cells similar to those described by James and often forming large aggregates devoid of a mucilage envelope.

(24) *Coccomyxa* A. Fig. 2e (S15, 18, 22, 27, 32, 33, 39). Cells ellipsoid-oblong ($5.5-7\mu$ l.; $1.5-2.0\mu$ br.) with widely rounded apices. Often in short irregular chains. The parietal chloroplast commonly covers only one side of the cell but sometimes as much as three-quarters of the surface. No pyrenoid.

(25) *Coccomyxa* B. Fig. 2f (S27, 33, 34, 39). Cells oval-oblong ($8-10\mu$ l.; $4-5\mu$ br.), generally in groups of two to four. The parietal chloroplast is of varied extent and contains a single pyrenoid.

(26) *Cylindrocystis Brebissonii* Menegh. (15). Maximum development on base-deficient soils. Petersen (1935, p. 161) does not consider it to be a true soil species but it occurs frequently in British soils (cf. Fritsch & John, 1942; John, 1942).

(27) *Dactylococcus bicaudatus* A.Br. (14). Mainly on acidic soils (cf. Fritsch & John, 1942, p. 380), but never common. Petersen (1935, p. 154; *Keratococcus bicaudatus* (A.Br.) Boye Pet.) states its main development is on aerial objects.

(28) *Dictyosphaerium minutum* Boye Pet. ((8), cultures only). Fig. 2m-q. The cells ($2.5-5\mu$ l.; $2.5-4\mu$ br.) are oval to subspherical with a parietal chloroplast covering a large part of the cell surface and a single pyrenoid. On division into two or four daughter cells, the mother-cell wall splits into four flaps to the points of which the daughter cells are usually lightly attached, though unattached cells are not uncommon. The colonies may contain over 200 cells. Petersen (1932, p. 37) states that previous authors have described a similar type of division in *Chlorella*, but the daughter cells never remain attached to the mother-cell wall. Isolated cells are similar to those of *Chlorella* in structure but, in my specimens, were generally more oval.

This species, new to Britain, has been observed in Denmark (Petersen, 1932, p. 154). *Dictyosphaerium terrestre* Fritsch & John (1942, p. 378) differs in the larger cells (up to 15μ diam.) and the thin thread-like connecting strands.

(29) *Gloeocystis* sp. (S27, 32, 34, 39).

(30) *Fernandinella alpina* Chodat and var. *globosa* Fritsch & John (1942, p. 380) (8). Never common. The species is known from Switzerland and Denmark (Petersen, 1935, p. 152) and the variety, to which some of the specimens belonged, from British soils.

(31) *Gongrosira terricola* Bristol (incl. *G. australis* Phillipson) (6). Fig. 3a-h. There is a central group of rounded cells, either separate or loosely attached to form short

filaments. In the latter case, crushing under a coverslip causes the short filaments to break up into separate cells. From this central system a number of short, little-branched filaments radiate outwards or, in a large tuft, somewhat upwards. The basal rounded cells reach 22μ in diameter while the outer cells of the filaments are usually one and a half times to twice as long as broad, reaching 21μ long. Their width varies between $7-15\mu$. The single parietal chloroplast covers a variable amount of the inner surface of the wall; the margins are rounded and often lobed. There is a single round pyrenoid. Very little starch is formed.

Sporangia (Fig. 3c) are generally formed in the basal cells; sometimes they are intercalary in the radiating outer filaments. In one case (S8) all the cells formed sporangia (Fig. 3h). The zoospores (Fig. 3f) escape through a large pore in the wall which varies in size and position. Prior to liberation they are olive green in colour and spherical. On liberation they become green and elongate ovoid ($11-12\mu$ l.; $4-5\mu$ br.). The two flagella are as long as or rather longer than the cell. There is a single lateral chloroplast but no pyrenoid. The narrow stigma is rather variable in position, lying somewhat anterior or posterior to the middle of the cell (Fig. 3f). Occasionally, most of the sporangia produce aplanospores which are usually numerous and develop to form chlorococcoid growths (Fig. 3g, h). Any or all of the cells of a plant turn into aplanosporangia. In the latter case, the largest basal cells do so first and produce the largest number of aplanospores, while the smaller outer cells turn into sporangia last and produce relatively few aplanospores. Transferring such sporangia from agar to distilled water before dehiscence often causes them to function as zoosporangia. Sometimes both types of sporangia are produced in the same plant on agar. It is clear, therefore, that aplanosporangia are arrested zoosporangia.

There is some disagreement in the description of this species. The descriptions of the dehiscence of the sporangia given by Bristol and James differ. Bristol (1920, p. 78) states there is a minute lateral aperture. James (1935, p. 533) states that there is a terminal aperture or irregular rupture of the wall. In each case (James, 1935, Fig. 5h, i) the aperture is not necessarily minute.

James describes the pyrenoid as ellipsoid. Bristol's figures suggest it is oval to sub-spherical. Bristol does not describe the zoospores but, from James's description and figures, they are clearly variable in shape, though commonly elongate ovoid. She states that the stigma is anterior.

In Phillipson's (1935, pp. 279-80) *G. australis* only aplanospores are formed and any larger cell is apparently capable of turning into a sporangium. Since my specimens show all gradations between zoosporangia and aplanosporangia, and either localized groups or all the cells may become sporangia, these features do not constitute a fundamental difference. *G. australis* should, therefore, be merged into *G. terricola*.

It may be doubted whether this alga should be placed in *Gongrosira* or *Pleurastrum*. It shows a close approximation to *Pleurastrum terrestre* Fritsch & John (1942, pp. 383-4) in the type of filamentous stage formed, in the cell shape, size and structure (apart from the absence of the large oil globule) and in the zoospores. Aplanospores also occur in *P. terrestre*, though the figures (Fritsch & John, 1942, Fig. 5q, r) show them to be of variable size. The formation of a basal 'pseudoparenchymatous' cushion or disk with filaments radiating from it, considered as a generic characteristic of *Gongrosira* (Printz, 1927, p. 204), is not strongly developed in this species. Generally the cells radiate

outwards, and only in profuse growths is there any sign of the production of more or less upwardly directed filaments. Bristol's plants hardly support her description of the central system as 'pseudoparenchymatous' (e.g. Bristol, 1920, Pl. II A). *Pleurastrum terrestre* appears to form an equally compact central system (e.g. Fritsch & John, 1942, Fig. 5i). The only difference between the two seems to lie in the formation of pleurococcoid growths in *Pleurastrum*. These are not described for *Gongrosira terricola* by Bristol, James or Phillipson nor were they seen by me. James (1935, p. 535, Fig. 6c) and Fritsch & John (1942, p. 385) describe such growths for *Pleurastrum*, though the latter authors state that they were less common than the filamentous or more or less chlorococcoid growths. If such growths are observed in *Gongrosira terricola*, there would seem no valid reason for separating it from *Pleurastrum*. Recorded from England (Bristol, 1920; James, 1935), India (Singh, 1939).

(32) *Hormidium flaccidum* A.Br. sensu lato and *H. nitens* Menegh. emend. Klebs. (46). *Hormidium nitens* only differs from *H. flaccidum* in forming a silky growth at the surface of liquid cultures (Klebs, 1896, p. 327). Hence, in the present survey where only moistened soil and agar plates were used, distinction was rarely possible. Similarly, under natural conditions, *H. nitens* cannot be distinguished by direct observation. Even under cultural conditions it is doubtful whether Klebs's distinction is trustworthy (cf. Petersen, 1915, p. 376). There can be little doubt that the two species have been confused by soil workers (Brand, 1913, p. 67, provisionally unites the two species).

A few of my specimens produced silky growths on moist agar. The rest are tentatively placed under *H. flaccidum* and occurred on soils of very diverse constitution. Even if these two species are distinct, it is still possible that there are a number of physiological races (cf. Strøm, 1928). It will, therefore, be necessary to examine the soil *Hormidia* critically before it can be substantiated that one or both these species are tolerant of such a wide variety of ecological conditions as this and other investigations suggest. Early workers (Piercy, 1917; Bristol, 1920; Fritsch, 1922a) record *H. flaccidum* from many British soils; later ones (James, 1935; Fritsch & John, 1942) only *H. nitens* on every soil. Bristol (1920) records *H. nitens* once, while *H. flaccidum* (Petersen, 1935, places her *Ulothrix subtilis* var. *variabilis* here) was very common. Petersen (1935) only records *Hormidium flaccidum*. If Phillipson be right in including the *Ulothrix subtilis*, *U. tenerrima* and *U. variabilis* of Gisl (1931-2, 1933), Moore & Karrer (1919) and Moore & Carter (1926) in *Hormidium flaccidum*, then this species occurs on a large number of diverse types of soil in Denmark, east Greenland, Germany and America as well as Australia (Phillipson, 1935).

(33) *Hormidium mucosum* Boye Pet. (1915; ? *Ulothrix tenuissima* Kütz., sensu Bristol, 1920, p. 76). Fig. 4a-i.

This species, new to Britain, occurred on twelve soils of diverse type in company with *H. flaccidum* (Kütz.) A.Br. sensu lato. I agree with Petersen (1935, p. 158) that it is quite distinct from *H. flaccidum*. The two-layered wall, when present, is characteristic; in its absence, it can be distinguished by its broader cells (9-22 μ l.; 15-20 μ br.). It differs from *H. crenulatum* Kütz. (Fritsch & John, 1942, p. 383) in the general presence of a two-layered wall which is not stratified. The outer layer of the wall is mucilaginous and very varied in extent and appearance (Fig. 4a-f, h). When it is absent (Fig. 4g) the filaments are indistinguishable from Bristol's *Ulothrix tenuissima* Kütz. (1920, text-fig. 12). It may be present on some of the cells and absent on others in the same filament. As in Petersen's

(1915), specimens, the outer layer dissolves in chlor-zinc-iodide without giving a cellulose reaction; a distinction from *Hormidium crenulatum* Kütz. Its surface is usually irregular. Fragmentation of the cells appears to take place as a result of the separation of the middle lamella. Sometimes the separated cells remain within the outer layer (Fig. 4d). This appearance may be the explanation of Petersen's (1915, p. 376) statement that, in contrast

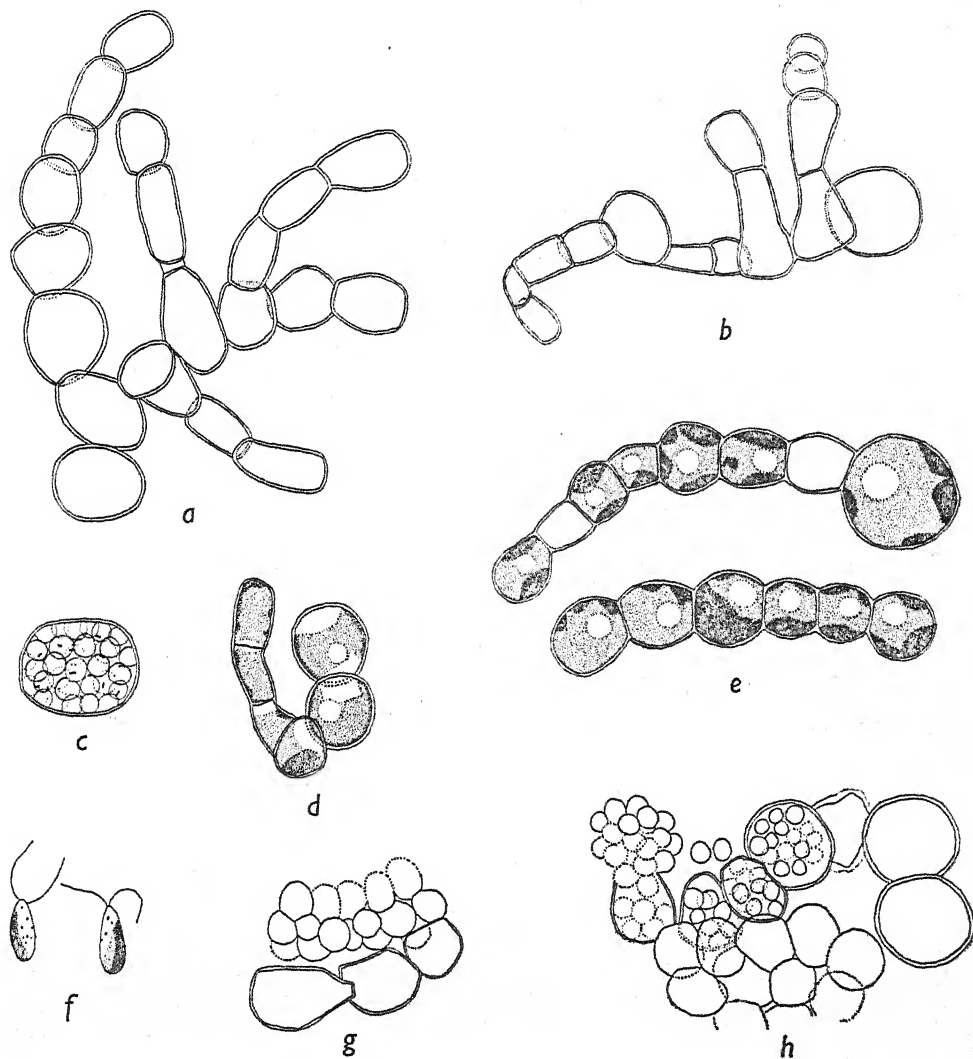


Fig. 3. *Gongrosira terricola* Bristol. *a, b, d, e* parts of thallus; *c*, zoosporangium; *f*, zoospores; *g, h*, aplanosporangia and chlorococcoid stages. *f*, $\times 1000$; rest, $\times 730$.

to *H. flaccidum*, the filaments do not dissociate by dissolution of the middle lamella. According to him, the filaments break in half and the broken cellulose membranes form tubiform prolongations to these two halves. Sometimes the outer layer forms large swellings at the points of separation of the cells (Fig. 4f). These are reminiscent of the plugs described for *Ulothrix zonata* (Web. & Mohr) Kuntz by Jane & Woodhead (1941).

The chloroplast is band-shaped but very variable in extent. A pyrenoid, though commonly present, is not always visible even after staining (Fig. 4c). Starch and oil are stored. The formation of motile reproductive cells was not observed. In one cell (Fig. 4i) the chloroplast divided into six portions, each with a pyrenoid, but, though kept under observation for several weeks, no further development took place. Recorded from Denmark and France (Petersen, 1935). *Hormidium mucosum* Korshikov (1941, p. 40) differs in the very thick (to 35μ) mucus envelope.

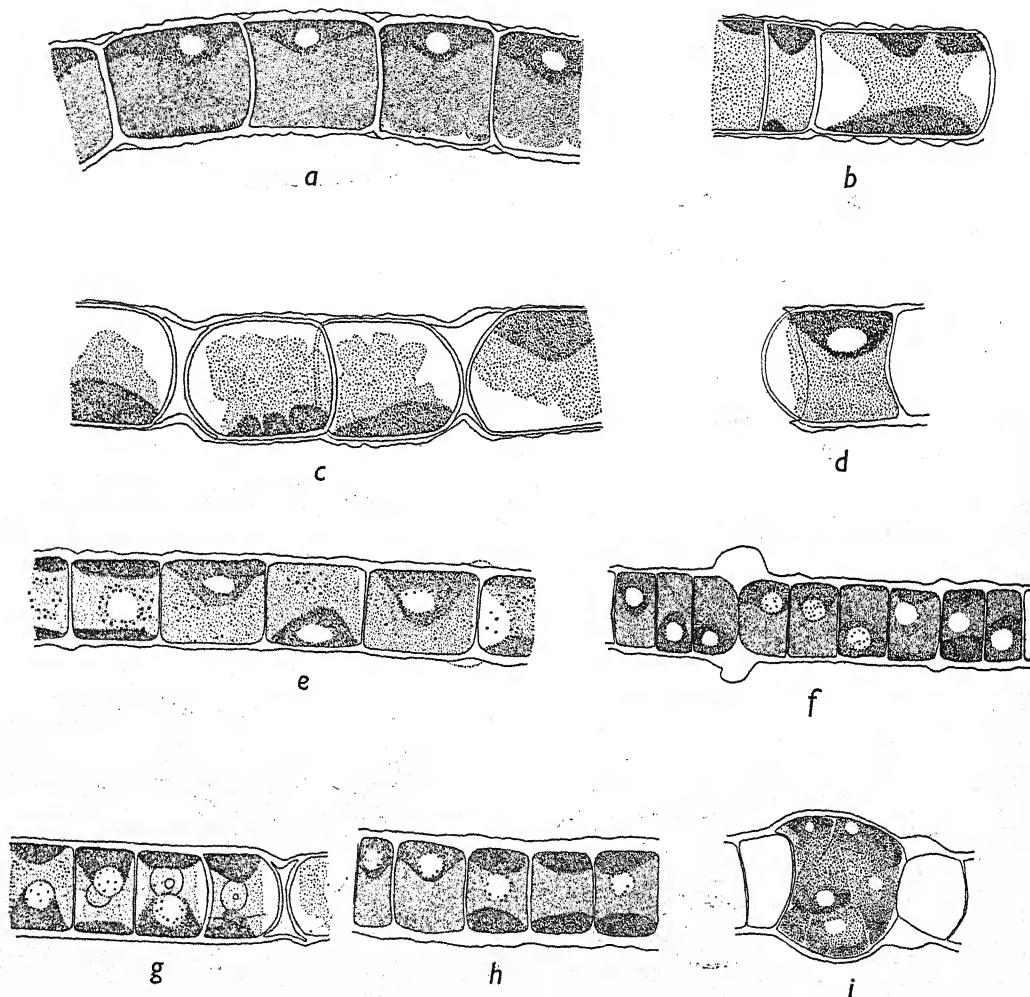


Fig. 4. *Hormidium mucosum* Boye Pet. a-d, $\times 1000$; e-i, $\times 730$.

- (34) *Macrochloris dissecta* Korsch. (8). Recorded by Fritsch & John (1942, p. 377).
 (35) *Mesotaenium violescens* De Bary (S22, 25, 27, 33).
 (36) *Muriella* sp. Small cells (up to 11μ diam.) belonging to this genus occurred on S30 (Fig. 2d). These were larger than *M. terrestris* Boye Pet. (Petersen, 1932) but never as large as *M. australis* Phillipson or *M. magna* Fritsch & John (1942).

(37) ? *Pleurastrum insigne* Chod. var., James (1935, p. 534). Pleurococcoid groups of cells resembling those described by James occurred on S₁₃ and 36.

(38) *Prasiola crispa* (Lightfoot) Menegh. (11); in the *Hormidium* form only. The foliose form is commonly produced where there are abundant supplies of nitrogen (especially rocks fouled by bird faeces) but was only once observed by Petersen (1935) in Denmark.

(39) *Stichococcus bacillaris* Näg. (21). On soils of varied type. Well known from terrestrial and aerial habitats (Petersen, 1935, p. 158). Probably an aggregate species (Chodat, 1928; Rath, 1938).

(40) *Trochiscia aspera* (Reinsch) Hansg. (S₂₉). Bristol (1920, p. 74) found it in thirty-four soils while the cells sometimes lacked the characteristic markings. *Trochiscia* stages are known in the life histories of various algae (cf. *Chlorococcum*, Fritsch & John, 1942, p. 376).

(41) *Vaucheria hamata* Walz. (6).

(42) *Vaucheria sessilis* (Vauch.) DC. (2).

(43) *Vaucheria geminata* DC. (1).

(44) *Vaucheria terrestris* (Vauch.) Lyngb. (1). Vegetative specimens of *Vaucheria* spp. occurred on fourteen soils.

(45) *Zygogonium ericetorum* (Roth.) Kütz. (8). On highly acid and base-deficient soils. It is well known from peaty soils, particularly those which are flooded in winter (Petersen, 1935).

(3) *Xanthophyceae*

(46) *Botrydiopsis anglica* Fritsch & John (1942, p. 389) (12). The only member of the class to grow on acid base-deficient soils. Well known from British soils (James, 1935; Fritsch & John, 1942).

(47) *Bumilleriopsis Peterseniana* Visch. & Pascher (Fig. 2r) (7). On alkaline, more or less markedly calcareous soils.

(48) *Heterothrix exilis* (Klebs) Pascher (20). Rarely seen by direct observation. A very common terrestrial alga (Petersen, 1935).

(49) *Heterococcus Chodati* Vischer (6). On alkaline soils. Well known from British soils (James, 1935; Fritsch & John, 1942).

(50) *Pleurochloris* sp. (4). Cells apparently belonging to this genus.

(51) *Tribonema bombycinum* (Ag.) Derb. & Sol. Alkaline soils (S₁, 2, 3, 8, 21).

(52) ? *Bumilleria* sp., Fig. 5a-l. This doubtfully filamentous alga belongs to this class by virtue of the storage of fats, absence of starch, blue colour when treated with conc. HCl and yellow-green chromatophores. The cells may be solitary or united into short threads. The latter state usually occurs when active division is taking place and it is rare to find more than two full-grown cells attached to one another. Even these can usually be squeezed apart under a coverslip. The adult cells are cylindrical, reaching 75 μ long. The breadth of all the cells is almost constant (11-13 μ). The adult cells contain up to twelve chromatophores but no pyrenoids. When such cells are kept under observation in moist chambers, they subdivide by transverse walls with or without an occasional longitudinal division (Fig. 5e-h, i-k). Four to eight daughter cells are formed within the mother-cell wall. The ends of the latter often remain attached to the end members of the chain of daughter cells. By repetition of this process, a series of two or three caps may be

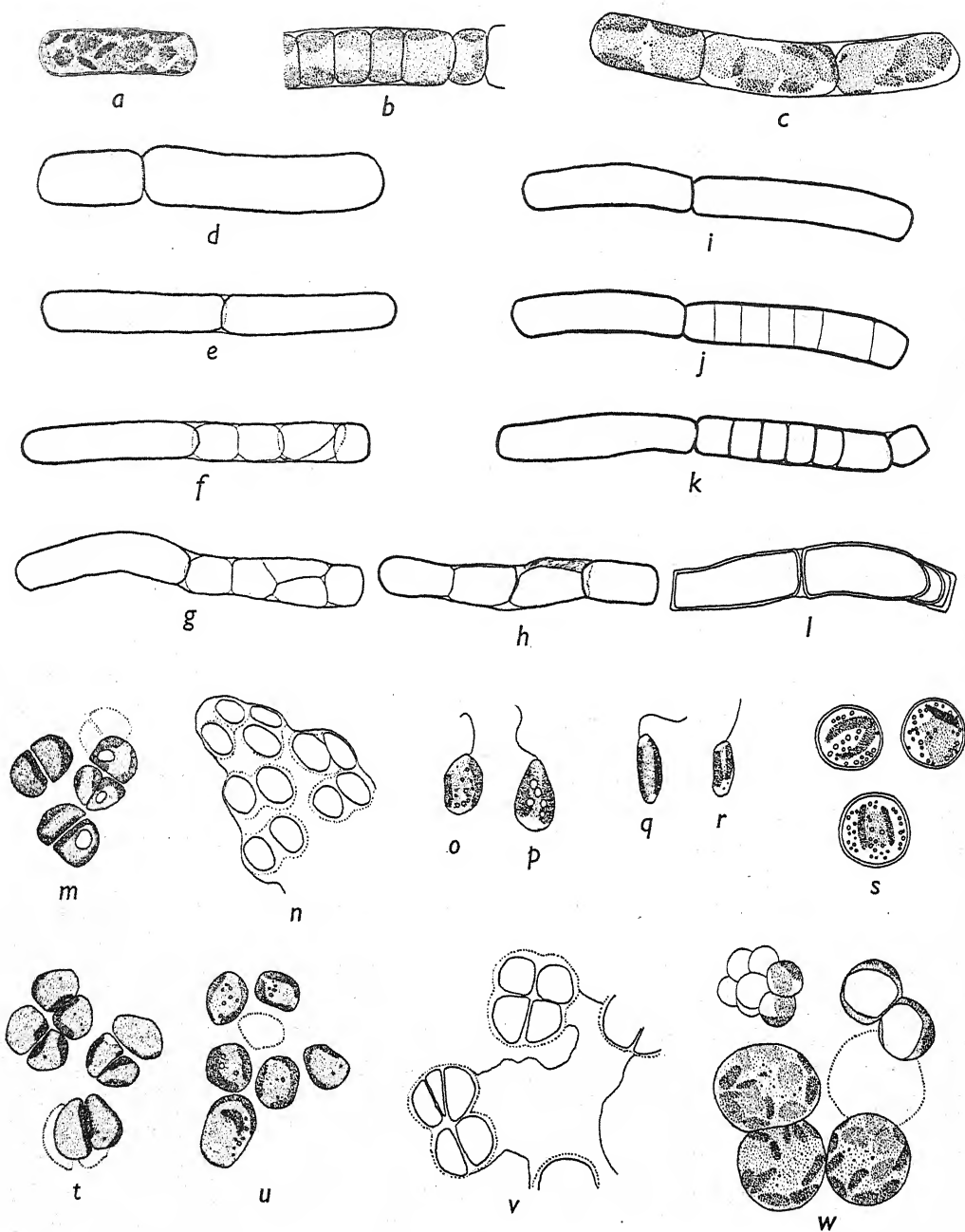


Fig. 5. *a-l*, ? *Bumilleria* sp.; *e-h* and *i-k*, stages in development of daughter cells; *f*, 7 days, *g*, 18 days, *h*, 49 days later than *e*; *g* and *h* seen from different view to *e* and *f*; *j*, 6 days, *k*, 11 days later than *h*; *l*, cell with caps. *m*, *o*, *p*, *u*, Chrysophyceae I; *n*, *q-t*, *v*, Chrysophyceae II; *w*, Chrysophyceae III; *o-r*, motile cells; *n*, *v*, colony in methylene blue; *w*, top left hand, daughter cells. *a*, *e-l*, $\times 450$; *b-d*, $\times 730$; *m-w*, $\times 1000$.

left attached to these cells (Fig. 5*l*). The young daughter cell (Fig. 5*b*) possesses only one chromatophore, the number increasing with the enlargement of the cell (Fig. 5*c*).

In the formation of short chains of cells as a result of division, this alga resembles *B. sicula* Borzi (Pascher, 1925, p. 110). It differs in the formation of caps to the end member of the daughter-cell series and the absence of H-pieces. It can be looked upon equally as a coccoid member of the class which forms chains of autospores. Until it is clear whether the middle lamella of the daughter cells is originally continuous with that of the parent cell or not, its exact status is doubtful. On one soil (S29).

(4) *Chrysophyceae*

Fritsch & John (1942, p. 391) have described as forms I-III, three terrestrial members of this class, two of which possessed *Ochromonas* swimmers. Two of the three seen by me possessed *Chromulina* swimmers. That there was only one flagellum was checked by staining. I have considered it best to describe these as forms I-III, as did Fritsch and John, for in none of them have cysts been observed.

(53) *Chrysophyceae* I (Fig. 5*m*, *o*, *p*, *u*). In the non-motile stage, there are small groups of naked subspherical to oval or oblong cells ($7-11\mu$ l.). No mucilage is formed. There is a parietal chromatophore covering a large part of the wall (Fig. 5*m*). Oil and leucosin are stored. Division occurs in three planes. Any of these cells may become motile when immersed in water. The motile cells ($12-13\mu$ l.; $5-6\mu$ br.) are oval to pyriform (Fig. 5*o*, *p*) and somewhat metabolic. The chromatophore is band-shaped. The flagellum is about as long as the cell. There is no stigma.

On three acid soils (S32, 35, 46).

(54) *Chrysophyceae* II (Fig. 5*n*, *q-t*, *v*). The non-motile cells ($6-12\mu$ l.; $4-5\mu$ br.) are similar in structure to those of the preceding alga (cf. Fig. 5*m*, *t*). They form large macroscopic groups embedded in mucilage (Fig. 5*n*, *v*). Division is in three planes. Occasionally, spherical cells ($6-10\mu$; Fig. 5*s*) with a firm wall were present in the mucilage masses. The wall was not silicified nor did it show any of the sculpturation common to cysts. Any of the naked cells can become motile on submergence. The motile cells ($8-10\mu$ l.; $3-4\mu$ br.) are ellipsoid to oblong (Fig. 5*q*, *r*), weakly metabolic and possess a flagellum about the length of the cell. There is no stigma.

On two acid soils (S46, 48).

(55) *Chrysophyceae* III (Fig. 5*w*). Only non-motile cells were observed. These occur in small groups without the production of mucilage. The individual cells (to 14μ br.) are more or less spherical and contain numerous discoid chromatophores. Examination in a moist chamber shows that they divide within the delicate membrane of the mother cell to form a sporangium. The daughter cells have only one chromatophore. Leucosin, often as large lumps, and oil are stored.

On three soils (S3, 29, 42).

(5) *Euglenineae*

(56) *Euglena mutabilis* Schmitz (10). Only on acid soils. It is known from acid soils (Fritsch & John, 1942, p. 394), mud, and temporary pools (Lund, 1938, 1942).

(57) *Euglena* sp. (Fig. 6*a-p*). In contrast to the above, this species occurred almost always on alkaline soils (seventeen samples).

The cells ($46-66\mu$ l.; $10-13\mu$ br.) are rounded anteriorly and pointed posteriorly. They are faintly striated (Fig. 6*a*). Though metabolic, they swim actively when free water is

present. The chromatophore consists of a thin parietal film covering a large part of the wall. This is thickened by folds at various places especially near the centre of the cell over the pyrenoid. These lobes are often arranged more or less radially giving the appearance of a stellate chromatophore (Fig. 6e, f). Under these conditions, the alga



Fig. 6. *Euglena* sp. m, mucilage. a, $\times 450$; b-h, j-k, m-p, $\times 730$; i, l, $\times 1000$.

resembles *E. viridis* Ehr. It is not clear whether the chromatophore does cover the pyrenoid or not, though some non-motile cells suggest that it does make contact with it (Fig. 6l, n). When the folds are poorly developed, there is a superficial resemblance, particularly in slender specimens,* to *E. mutabilis* (cf. Fig. 6j, k). The central pyrenoid is often hidden by paramylon, oil or the folds of the chromatophore. Even in the absence

* Possibly these belong to another species.

of these it may not be visible (Fig. 6*b-f*). The anterior stigma is saucer-shaped. Red-brown granules may occur at various places in the cell. The large oval-oblong nucleus lies near the centre of the cell or posteriorly. Oval (Fig. 6*l, o, p*) resting stages often occur and are generally formed when it is kept for prolonged periods in a moist chamber. They may reach 26μ diam. A thin layer of mucilage surrounding them is often detectable (Fig. 6*o*) and strands from the peripheral part of the chromatophore pass to the central pyrenoid. Division occurs in this stage leading to groups of two to four cells (Fig. 6*m, n*).

The *E. viridis* of Bristol Roach (1927) may belong here. Dr Pringsheim has examined my figures and specimens and states that he is unable to name this species in the absence of cultural work but that it appears to belong to the forms grouped under *E. viridis* Ehrenb.

D. SUMMARY

The algal flora, exclusive of diatoms, on fifty-four diverse soils has been examined by direct observation and cultures.

The flora of the highly acid soils consists exclusively of Chlorophyceae, which are also the most abundant class on base-deficient soils generally. On the more alkaline soils and those which are not base-deficient, Chlorophyceae are frequently abundant but may be replaced by Myxophyceae or Bacillariophyceae.

Myxophyceae occur in quantity on soils which are not base-deficient, contain nitrates and are rich in phosphates.

The species showed varying toleration to base-deficiency and pH. Certain Chlorophyceae are calcifuge and most Myxophyceae and Xanthophyceae calcicole.

The results of the present survey are compared with those of previous investigations.

On one soil, examined over five years, no seasonal succession of species occurred. The numbers of algae in this soil varied in relation to the weather conditions. Most species appear to be surface forms but the difference in frequency of Xanthophyceae, as found by direct observation and cultural methods, may be related to micro-stratification.

The taxonomy of some of the species occurring on the soils is considered.

The author's grateful thanks are due to Professor F. E. Fritsch for advice and criticism and to Professor J. M. Webster, in whose laboratory most of the work was carried out.

APPENDIX
Table 2. *The chemical analysis and productivity of the soils*

Phosphate and potash contents, actual amounts; no allowance made for organic matter (Lund, 1945, p. 202). Calcium deficiency, when present, scale of X-5X used to indicate intensity of colour produced by Comber-Misra test; nitrates, when present, scale of 1-4 used to indicate intensity of colour produced by Pearsall's method (diphenylamine, Lund, 1945, p. 198). For estimation of productivity numbers see Lund, 1945, p. 202. Tr. = trace.

Soil no.	39	22	32	33	34	40	15	27	35	14	48	25	7	10	17
pH	3.7	3.9	4.4	4.4	4.4	4.4	4.4	4.6	4.8	4.7	4.7	4.8	4.8	5.0	5.1
Ca deficiency	5X	5X	4X	4X	4X	4X	4X	5X	2X	3X	2X	4X	4X	4X	5X
CaCO ₃	0.006	0.003	0.018	0.002	0.014	0.015	0.026	0.004	0.006	0.027	0.008	0.004	0.021	0.082	0.011
NO ₃	0.017	0.011	0.002	0.004	0.014	0.021	0.019	0.003	0.009	0.025	0.005	0.007	0.010	0.21	0.011
PO ₄ (P ₂ O ₅)	37.2	20.6	18.1	13.9	17.8	11.0	51.3	26.3	8.9	29.4	17.0	20.0	8.9	15.8	31.0
Organic matter	0	0	1	2	1	1	10	4	5	28	15	3	32	4	15
Bacillariophyceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chlorophyceae	20	23	0	36	6	25	4	37	3	0	21	11	36	18	4
Myxophyceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chrysophyceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Xanthophyceae	0	1	2	0	0	0	0	1	0	0	1	1	2	0	0
Euglenineae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Total	20	34	25	38	7	26	14	42	8	29	45	14	74	22	33
Soil no.	50	9	46	12	28	49	6	13	58	18	38	11	16	57	20
pH	5.1	5.2	5.2	5.3	5.3	5.4	5.5	5.6	5.6	5.9	5.9	6.0	6.2	6.2	6.4
Ca deficiency	1X	3X	1X	1X	3X	1X	Tr.	1X	0.09	2X	Tr.	Tr.	Tr.	Tr.	Tr.
CaCO ₃	0.011	0.009	0.001	0.030	0.008	0.004	0.042	0.015	0.005	0.028	0.005	0.058	0.053	0.072	0.012
NO ₃	0.010	0.007	0.016	0.011	0.018	0.012	0.019	0.018	0.009	0.006	0.013	0.015	0.010	0.025	0.012
PO ₄ (P ₂ O ₅)	7.5	5.4	13.3	11.6	4.8	7.4	9.1	5.3	7.8	4.6	8.7	7.0	6.7	12.5	14.0
Organic matter	4	14	5	13	8	5	24	10	14	7	23	50	22	39	30
Bacillariophyceae	5	65	19	31	18	9	37	0	—	4	15	20	52	21	50
Chlorophyceae	0	0	1	0	0	3	2	0	—	0	0	0	0	0	0
Myxophyceae	0	0	0	0	0	0	0	0	—	0	0	0	0	0	0
Chrysophyceae	0	0	0	0	0	0	0	1	—	0	0	0	0	0	0
Xanthophyceae	0	0	0	1	0	0	2	1	—	0	0	0	0	0	0
Euglenineae	0	8	0	0	0	0	0	0	—	0	0	0	0	0	0
Total	9	87	25	45	26	19	65	20	—	11	39	91	74	60	80
Soil no.	10	4	3	45	31	24	2	41	5	8	21	29	30	54	23
pH	6.4	6.4	6.4	6.4	6.4	6.6	6.6	6.7	6.9	6.9	7.0	7.0	7.1	7.1	7.1
Ca deficiency	Tr.	Tr.	Tr.	Tr.	Tr.	Tr.	Tr.	Tr.	Tr.	Tr.	Tr.	Tr.	Tr.	Tr.	Tr.
CaCO ₃	0.014	0.083	0.075	0.021	0.073	0.003	0.093	0.025	0.013	Tr.	Tr.	Tr.	0.12	4.4	0.45
NO ₃	0.004	0.008	0.019	0.010	0.008	0.010	0.025	0.022	0.04	0.008	0.008	0.172	0.030	0.198	0.06
PO ₄ (P ₂ O ₅)	5.9	14.5	13.0	6.3	8.1	11.2	15.7	13.7	5.9	10.3	>0.02	10.1	7.0	12.1	14.1
Organic matter	4	34	47	36	44	28	26	7	41	14	20	76	32	41	3
Bacillariophyceae	0	0	0	—	13	14	0	0	21	26	24	7	2	40	2
Chlorophyceae	0	0	1	—	13	1	0	0	5	3	9	30	26	1	1
Myxophyceae	0	0	0	—	0	0	0	0	0	0	0	0	0	0	0
Chrysophyceae	0	0	0	—	0	0	0	0	0	0	0	0	0	0	0
Xanthophyceae	0	0	0	—	0	0	0	0	1	0	0	8	0	1	0
Euglenineae	0	1	1	—	1	0	4	0	0	0	2	0	0	0	0
Total	4	46	97	—	76	43	30	16	68	43	55	121	60	83	6
Soil no.	55	26	52	1	44	53	36	47	56	37	42	43	51	51	51
pH	7.1	7.2	7.2	7.4	7.4	7.4	7.4	7.5	7.6	8.0	8.2	8.2	8.3	8.3	8.3
Ca deficiency	Tr.	Tr.	Tr.	Tr.	Tr.	Tr.	Tr.	Tr.	Tr.	Tr.	Tr.	Tr.	Tr.	Tr.	Tr.
CaCO ₃	0.004	0.009	0.046	0.013	0.014	0.027	0.011	0.080	0.005	0.021	0.015	0.041	0.060	0.060	0.060
NO ₃	0.014	0.019	0.013	0.025	0.014	0.011	0.020	0.014	0.009	0.021	0.015	0.007	0.060	0.060	0.060
PO ₄ (P ₂ O ₅)	11.9	16.6	22.6	8.8	6.9	5.3	3.6	15.9	10.4	21.2	9.8	8.6	9.4	9.4	9.4
Organic matter	5	8	55	23	29	36	6	30	4	36	6	3	24	24	24
Bacillariophyceae	16	13	—	16	0	4	0	23	17	22	3	1	—	—	—
Chlorophyceae	13	4	—	9	0	4	0	0	1	4	0	0	—	—	—
Myxophyceae	1	0	—	0	0	0	0	0	0	0	0	0	—	—	—
Chrysophyceae	1	0	—	0	0	0	0	0	0	0	0	0	—	—	—
Xanthophyceae	0	1	—	0	0	1	0	0	0	0	0	0	—	—	—
Euglenineae	0	0	—	0	0	1	0	0	0	0	0	0	—	—	—
Total	4	18	—	48	56	50	39	55	23	62	10	4	—	—	—

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GEOGRAPHICAL AND OTHER ABBREVIATIONS IN THE *FLORA U.R.S.S.* BY KOMAROV AND OTHERS

By WILLIAM T. STEARN

Lindley Library, Royal Horticultural Society, London

(With 4 figures in the text)

The Union of Soviet Socialist Republics occupies over 8 million square miles. So vast an area naturally offers plants a great diversity of environmental conditions and accordingly possesses a rich varied flora estimated in 1934 to comprise between 15,000 and 20,000 species of flowering plants and vascular cryptogams. Of these Ledebour's *Flora Rossica* (1841-53; cf. Stearn, 1941), being written before the annexation of Western Turkistan to the Russian Empire, describes no more than 6600. Hence in 1931 plans were made for a new work embracing the whole Soviet Union. Prof. Vladimir L. Komarov was appointed general editor of this *Flora U.R.S.S.* (*Flora Unionis Rerumpublicarum Sovieticarum Socialisticarum*: Флора С.С.С.Р.), in the preparation of which at least forty-two Soviet botanists have now co-operated. Vols. 1-2 appeared in 1934, 3-4 in 1935, 5-6 in 1936, 7 in 1937, 8-9 in 1939, 10 in 1941, 11 in 1945. They follow Engler's system and describe the vascular cryptogams, gymnosperms and angiosperms from Typhaceae to Leguminosae. They are illustrated and include keys, detailed descriptions, summaries of geographical distribution and notes on economic uses. The whole work, except for scientific names, references and descriptions in Latin of new genera and species, is in Russian, and its information is accordingly not readily available to non-Soviet botanists, although since many species of the U.S.S.R. grow also in adjoining territories, such a work is extremely important for the study of the flora of Europe and northern Asia as a whole. Translations, of which Airy Shaw's (Vvedensky, 1946) may be taken as an example, are accordingly much to be desired, but even in their absence a person totally ignorant of Russian should be able to ascertain from the *Flora U.R.S.S.* the general distribution of any plant described therein. All that is required is study of the following list of abbreviations and care in matching the Cyrillic characters.

For the purpose of this *Flora*, Soviet territory has been divided into seven parts or major areas: the *Arctic*, from Kola Peninsula to Bering Strait; the *European*, extending south of the Arctic to the Black Sea, Caucasus and Caspian Sea; *Caucasus*, including Soviet Armenia and Azerbaijan; *Western Siberia*, including Soviet Altai; *Eastern Siberia*; the *Far Eastern* part from Kamchatka south to Vladivostok; *Central Asia*, corresponding to Russian (or Western) Turkistan of the Tsarist Empire. These are divided in all into forty-nine floristic regions or zones (районы) based on important topographical features such as mountain ranges, courses and basins of rivers, large deserts, inland seas, lakes and peninsulas. Only a few of them coincide in name and area with past or present administrative divisions (cf. Horrabin & Gregory, 1945). They are not mapped in any atlas, but a sketch-map in *Flora U.R.S.S.* 1, facing p. xvi (1934), indicates their approximate boundaries. In the text of the *Flora* they are cited by the same abbreviations of their Russian names as appear on this map and are listed in full and numbered in vol. 1, 13-14 (1934)

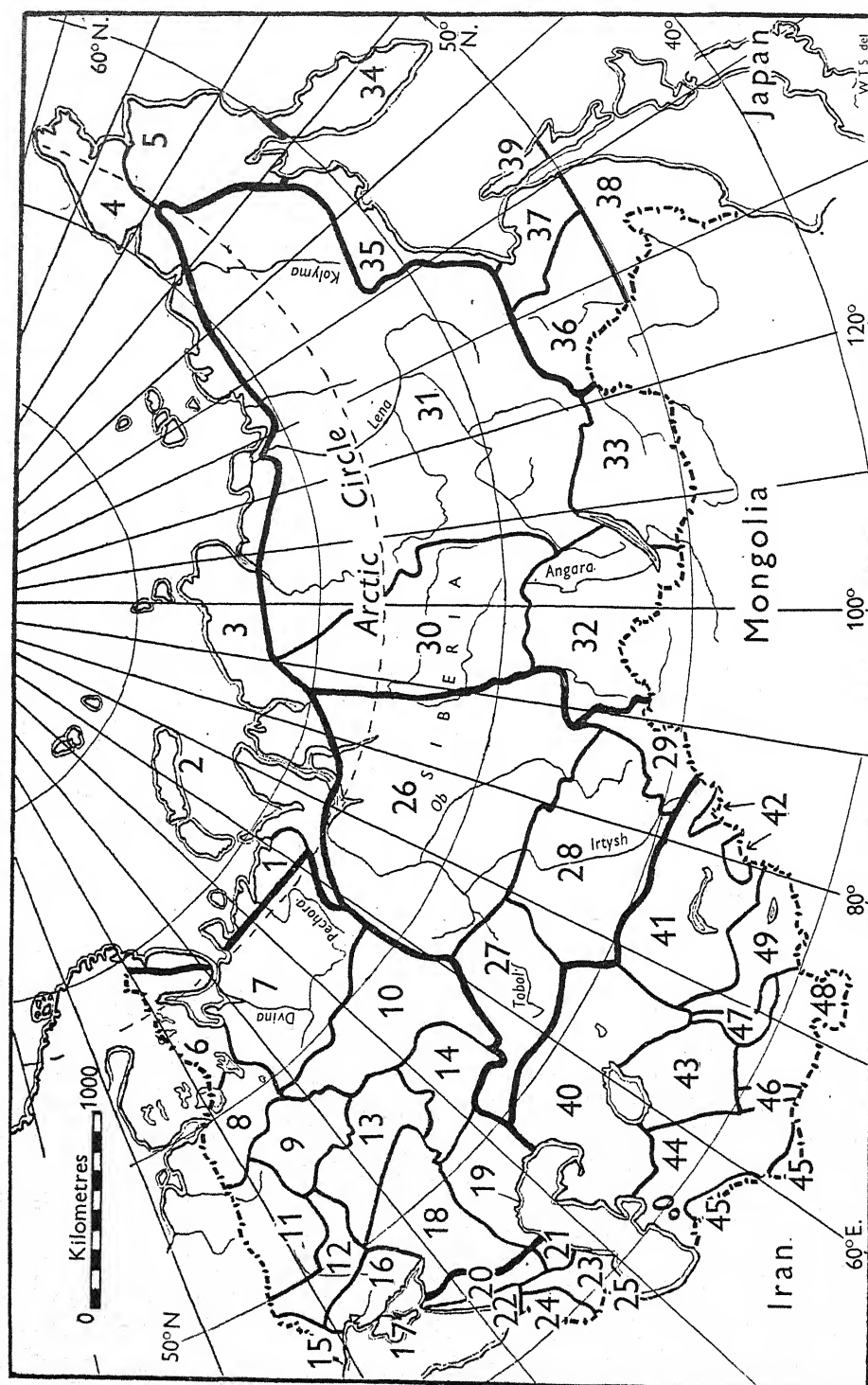


Fig. 1.

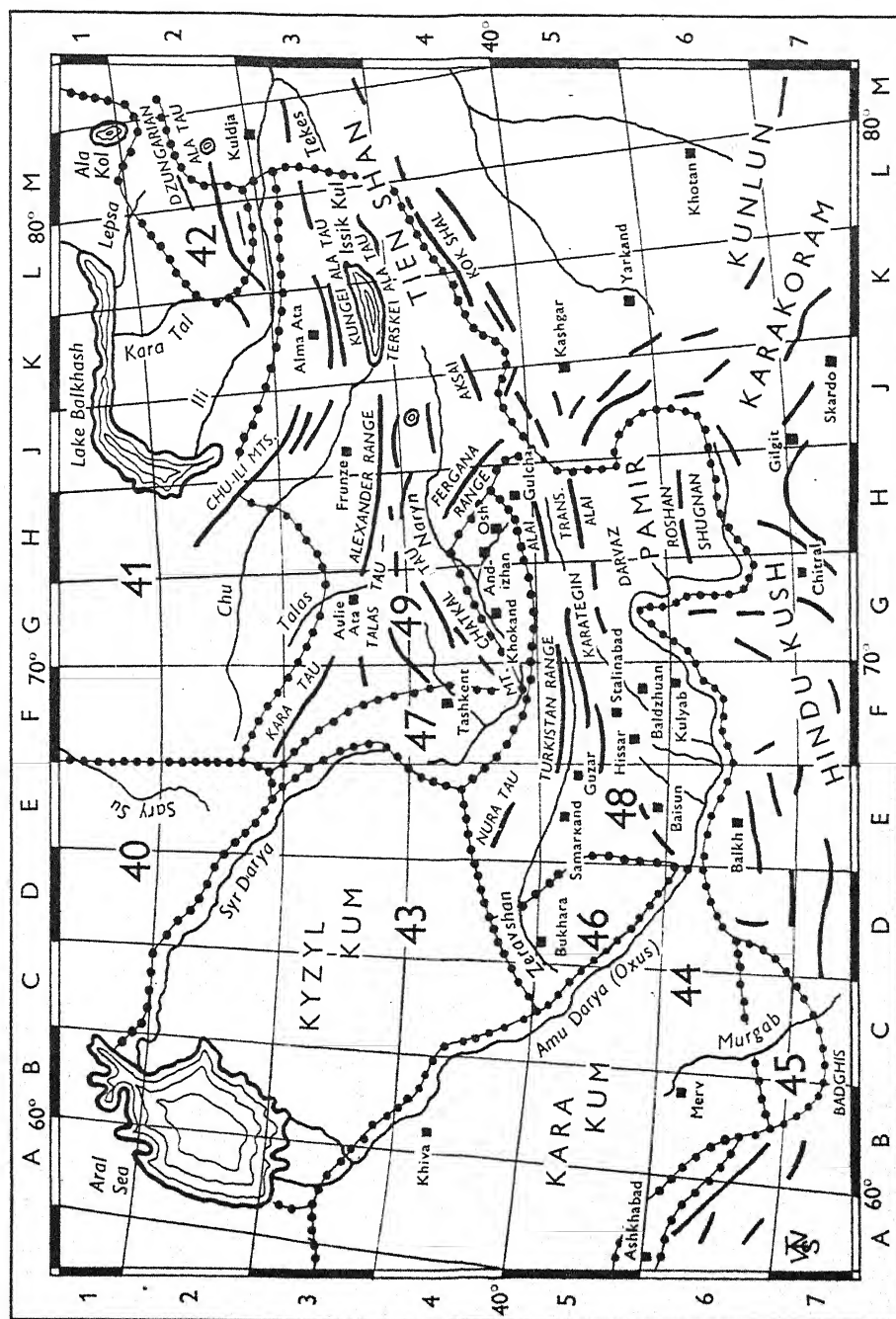


Fig. 2.

and *Index*, vols. 1-4, p. v (1936). The numbers used there have been substituted in Fig. 1, which is a small-scale copy of this map, for the Cyrillic characters of the original.

Hence, to understand a statement of distribution in the *Flora U.R.S.S.*, search the list below for the abbreviations used and then find the associated numbers on the maps (Figs. 1-3). Thus the distribution of *Allium ursinum* L. in U.S.S.R. is stated to be:

‘Европ. ч.: Верх.-Днепр., Сред.-Днепр., Волж.-Дон. (зап. ч.); Кавказ: Предкавк., Зап., Вост. и Южн. Закавк.’

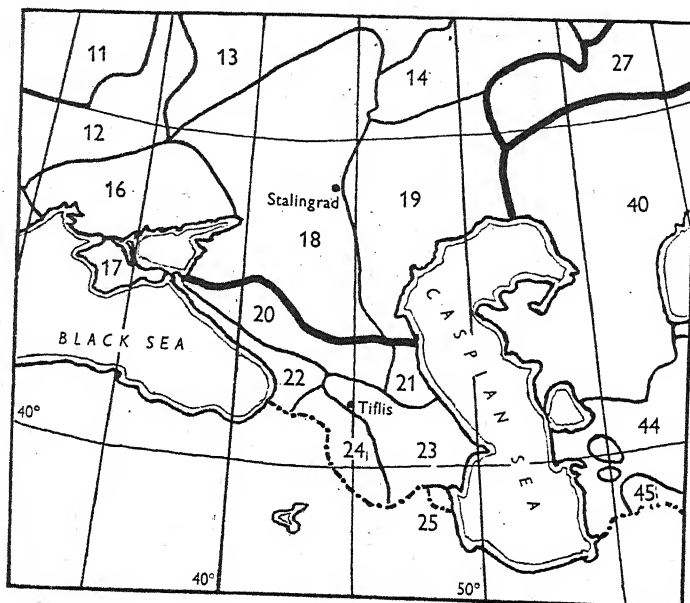


Fig. 3.

Study of the list shows that it occurs in regions 11-13, 20, 22, 23, which on reference to Fig. 1 are seen to be in south-west European Russia and the Caucasus.

I. АРКТ. ARCTIC	
1. Аркт. Евр.	Arctic Europe
2. Н. Зем.	Novaya Zemlya
3. Аркт. Сиб.	Arctic Siberia
4. Чук.	Chukotsk
5. Анад.	Anadyr
II. Европ. ч. EUROPEAN PART	
6. Кар.-Лапл.	Karelian Lapland
7. Дв.-Печ.	Dvina-Pechora
8. Лад.-Ильм.	Ladoga-Ilmen
9. Верх.-Волж.	Upper Volga
10. Волж.-Кам.	Volga-Kama
11. Верх.-Днепр.	Upper Dnieper
12. Сред.-Днепр.	Middle Dnieper
13. Волж.-Дон.	Volga-Don
14. Заволж.	Transvolga
15. Бесс.	Bessarabia
16. Причерн.	Black Sea
17. Крым.	Crimea
18. Ниж.-Дон.	Lower Don
19. Ниж.-Волж.	Lower Volga
19a. Урал.	Ural
III. Кавказ. CAUCASUS	
20. Предкавк.	Ciscaucasia
21. Даг.	Dagestan
22. Зап.-Закавк.	West Transcaucasia
23. Вост.-Закавк.	East Transcaucasia
24. Юж.-Закавк.	South Transcaucasia
25. Тал.	Talysh

IV. Зап. Сибирь. WESTERN SIBERIA

26. Обск.	Ob	28. Ирт.	Irtysk
27. Верх.-Тоб.	Upper Tobol	29. Алт.	Altai

V. Вост. Сибирь. EASTERN SIBERIA

30. Енис.	Yenisei	32. Анг.-Саян.	Angara-Sayan
31. Лен.-Кол.	Lena-Kolyma	33. Даур.	Dauria

VI. Дальн. Восток. FAR EAST

34. Камч.	Kamchatka	37. Удск.	Udsk
35. Охот.	Okhotsk	38. Уссури.	Ussuri
36. Зее-Бур.	Zeya-Bureya	39. Сах.	Sakhalin

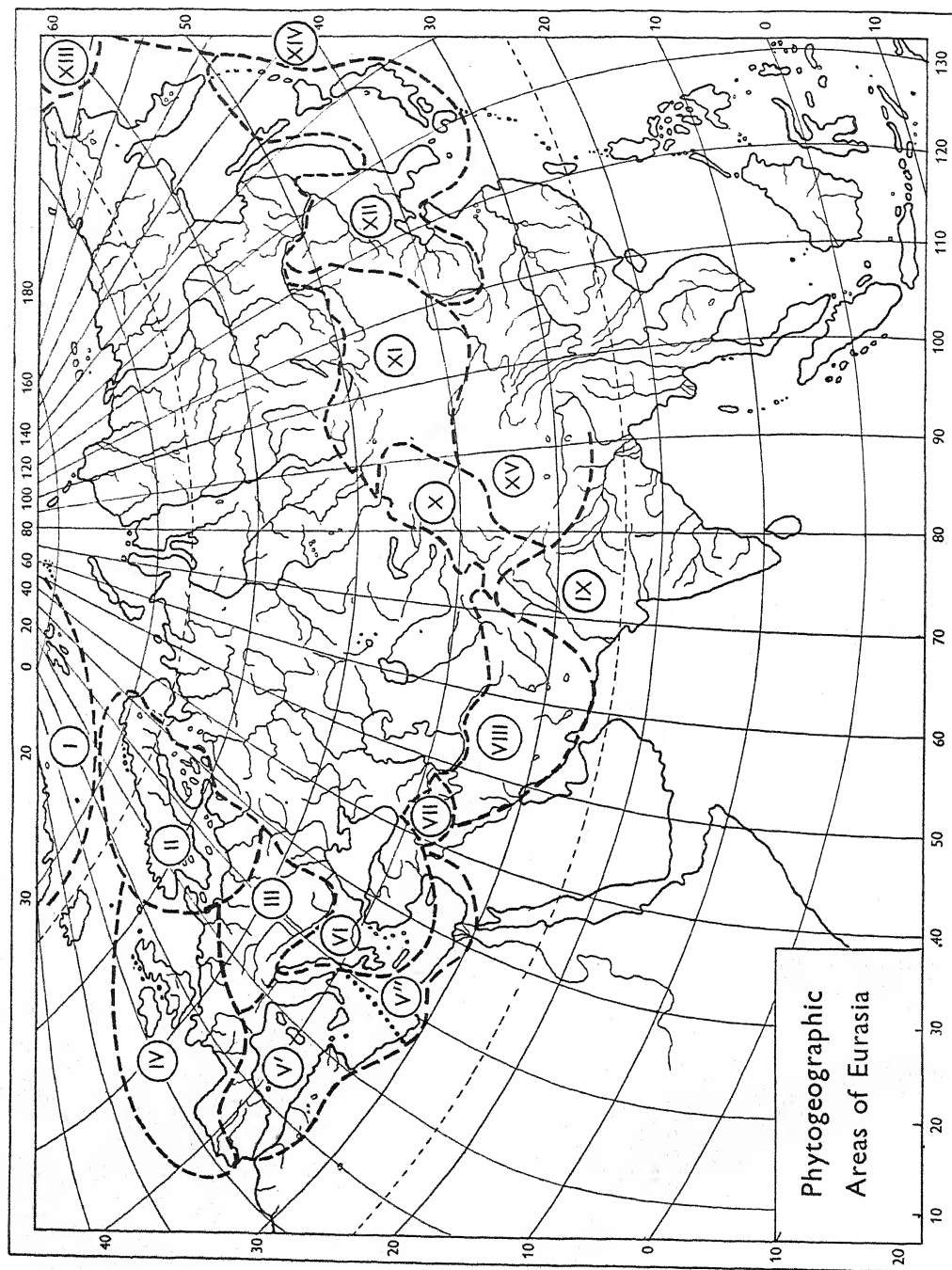
VII. Ср. Азия. CENTRAL ASIA

40. Арало-Касп.	Aralo-Caspia	45. Горн.-Туркм.	Mountain Turkmenia
41. Прибалх.	Balkhash	46. Аму-Дар.	Amu Darya foothills
42. Дж.-Тарб.	Dzungaro-Tarbagatai	47. Сыр-Дар.	Syr Darya foothills
43. Кыз.-Кум.	Kyzyl (Kizil) Kum	48. Пам.-Ал.	Pamir-Alai
44. Кара-Кум.	Kara Kum	49. Тянь-Шан.	Tien Shan

For indicating the general distribution (общ. распр.) of species which range beyond the Soviet Union, the following abbreviations (cf. Fig. 4) are employed:

I. Аркт.	Arctic, i.e. Spitsbergen and Greenland.
II. Сканд.	Scandinavia, i.e. Norway, Denmark, Sweden, Finland, Estonia, Latvia.
III. Ср. Евр.	Central Europe, i.e. Germany, Lithuania, Poland, Czechoslovakia, Hungary, Austria, Switzerland.
IV. Атл. Евр.	Atlantic Europe, i.e. Holland, Belgium, the British Isles, France, Portugal.
V. Средиз.	Mediterranean, i.e. (1) Spain, Italy, Algeria, Tunisia, Tripolitania; (2) Cyrenaica, Egypt, Palestine, Syria.
VI. Балк.-Малоаз.	Balkan Peninsula and Asia Minor.
VII. Арм.-Курд.	Turkish Armenia and Kurdistan.
VIII. Иран.	Iran, i.e. Persia and Afghanistan.
IX. Инд.-Гим.	India and the Himalaya.
X. Дж.-Кашг.	Eastern (or Chinese) Turkistan, i.e. Kuldja district, Dzungaria and Kashgaria.
XI. Монг.	Mongolia.
XII. Японо-Кит.	Japan and China, i.e. northern China, Manchuria, Korea, Japan, south Sakhalin (Karafuto) and Kurile Islands.
XIII. Беринг.	Beringia, i.e. Alaskan (or eastern) coast of Bering Sea.
XIV. Сев. Ам.	North America, i.e. Canada and U.S.A.
XV. Тиб.	Tibet.

Further details are given in a paper published elsewhere (Stearn, 1946). For gaining a general impression of geographical conditions in the Soviet Union, the works of Cameda d'Almeida, Gregory & Shave, and Horrabain & Gregory will be found very helpful.



The following abbreviations (of which Roman transliterations are given below in brackets) are used in descriptions:

вн. (vn.)	corolla	п. (r.)	plant	чшч. (chshch.)	calyx
зв. (zv.)	ovary	р.лц. (rlts.)	stigma	б.м. (b.m.)	more or less
клк. (klk.)	spike, ear	с. (s.)	seed	б.ч. (b.ch.)	for the most
кр. (kr.)	root	сцв. (stsv.)	inflorescence		part, mostly
крш. (krshch.)	rhizome	смшч. (smshch.)	ovule	выс. (vys.)	high
л. (l.)	leaf	ст. (st.)	stem	дл. (dl.)	long
лп. (lp.)	petal	стлб. (stlb.)	style	ок. (ok.)	circa
мшч. (mshch.)	utricle	тыч. (tych.)	stamen	рн. (rn.)	region
околоцв. (okolotsv.)	perianth	цв. (tsv.)	flower	шир. (shir.)	broad
пл. (pl.)	fruit	цвн. (tsvn.)	peduncle or pedicel	○	annual
плн. (pln.)	anther	цвтл. (tsvtl.)	receptacle	⊙	biennial
прицв. (pritsv.)	bract	чрш. (chrsh.)	petiole	∟	perennial
прлст. (prlst.)	stipule	чш. (chsh.)	scale	h	shrub
пст. (pst.)	gynoecium	чшл. (chshl.)	sepal	h	tree

The abbreviation 'A.H.P.' refers to the St Petersburg periodical *Acta Horti Petropolitani*; 'H.F.R.' to the specimens distributed in the *Herbarium Florae Rossicae*, and 'H.F.A.M.' to those in the *Herbarium Florae Asiae Mediae*.

Floristically the richest and most interesting parts of the Soviet Union are the Caucasus and Central Asia (cf. Stearn, 1946). Fig. 2 gives the approximate boundaries of the floristic regions of Central Asia as deduced from statements in the text of *Flora U.R.S.S.* 4. Fig. 3 showing the Caucasus and adjacent territory has been copied direct from the sketch-map in vol. 1, a few place-names being added. For phytogeographic purposes these Caucasian regions need further division, as proposed by Kusnezow (1909) and Grossheim (1936).

The help of Mr H. K. Airy Shaw and Mr M. Aourousseau in compiling the above lists is gratefully acknowledged.

SUMMARY

This paper provides lists and maps whereby anyone ignorant of Russian can, nevertheless, translate the geographic and other abbreviations of the *Flora U.R.S.S.* into English equivalents and ascertain the general distribution of species described in that work.

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THE RESPIRATION OF STRAWBERRY LEAVES ATTACHED TO THE PLANT

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(With 11 figures in the text)

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I. INTRODUCTION

The loss of vigour in strawberry plantations after the first three or four years of life of the plants is well known, and is reflected in the common practice of renewing the plantation every few years. The replacement has usually been achieved by the use of young plants developed from runners of the older plants which are scrapped. This would seem to imply that the individual strawberry plant loses its vigour after a few years, and that the young plants produced on the runners from the parent plant are subject to a rejuvenating influence which results in their reactivation to the original vigour of the parent plant in its early life. More recently, however, it has become recognized that the main cause of loss of vigour in older strawberry plantations is through the progressive infection of the plants with various forms of virus disease (Cheal, 1946; Harris, 1936; Harris & King, 1942). This interpretation of the loss in vigour of strawberry plantations is borne out by the observations of Wright & Ward (1929) that in the years before virus infection had become so devastating strawberry plantations in the Wisbech area often remained down for 10 or 12 years, and that these old plants were often thought to be more profitable.

The experiments forming the basis of this paper were started in 1937, before the predominant role of virus infection was established, and they were intended to explore the possibility of loss of physiological vigour with age, and reinvigoration at the runner stage. It has been shown that the respiratory index of plant tissues changes with the age of the plant (Kidd, West & Briggs, 1921; Singh, 1935), and also with the age of the particular organ investigated, so that the respiratory index of the leaves seemed to be an obvious criterion for determining the course of senescence in these plants. A method was evolved for measuring the CO_2 emission of individual strawberry leaves over 15 min. periods while the leaf remained attached to the parent plant, and this was used during

1939 and 1940 to make a preliminary survey of the changes in respiratory activity of individual leaves from plants of different ages from the time of emergence of the leaf to its death. The war prevented further development beyond this initial survey.

2. EXPERIMENTAL DETAILS

Cultivation. A number of plants of a virus-free strain were obtained from East Malling Research Station in 1937 and were grown in large pots which were either plunged in cinders in a cool greenhouse, or in the earth outside the laboratories. The plants in the greenhouse were watered at frequent intervals throughout the summer, and given 250 c.c. of a complete culture solution (James, 1936) every 14 days from March to October. Plants grown out of doors were only watered during hot, dry spells. All experimental plants were examined daily, and the time of first appearance of each leaf, inflorescence, and runner, was noted; also the time at which unfolding of the leaf lamina was begun and completed. Plants were numbered in such a way that the parent plant was known, and also the order of appearance of the runner, and the position in which the leaf grew on the runner.

No attempt was made to control the temperature or light intensity of the greenhouse, but a thermograph was used to obtain continuous records of the temperature fluctuations in the greenhouse. The temperature varied between 9 and 35° C., with a winter mean of 14° and a summer mean of about 25°. All respiration readings were taken with the leaf at a temperature of 24.5° C.

A close watch was kept for signs of virus infection, but disease was absent throughout the entire experimental period, although one plant was isolated for a time on suspicion of yellow edge.

Measurement of respiration. This required an elaborate assembly of apparatus which was set up in a well-lighted laboratory facing north so that the room kept fairly cool in the summer. The pot containing the plant to be used was removed from the greenhouse and placed in a special container to which the leaf chamber was rigidly attached. In this way the plant, with one leaf enclosed in the leaf chamber, could be immersed in the water-bath without appreciable movement of the plant relative to the enclosed leaf, so that the risk of snapping the petiole of the enclosed leaf was minimized. After the leaf chamber had been sealed the container was placed on a rack over the thermostatically controlled water-bath so that the leaf chamber was immersed in the water-bath, and the inlet and outlet ports of the leaf chamber were then connected up and the gas flow (of CO₂-free air at 24.5° C. and saturated with water vapour) was started. The whole operation took about 2 min. from the removal of the plant from the greenhouse.

Three titrations were performed at approximately 15 min. intervals, giving three successive estimations of the CO₂ emission of the leaf. The blank time between each titration period and the next (occupied in the completion of titration and renewal of baryta solution) was between 2 and 3 min., so that the plant was removed from the greenhouse for a total period of less than 55 min. on each occasion. Determinations on any one leaf were usually made every other day during the period of expansion, and weekly, or at longer intervals when the respiratory activity had ceased to alter very rapidly.

External air was led in to the laboratory through a sulphuric acid bubbler (which dries the air and prevents solidification of the soda lime) and a soda-lime tower into warming

coils immersed in the thermostatically controlled water-bath. After being warmed the (CO_2 -free) air was bubbled through distilled water and then led through the leaf chamber, or through a by-pass, to the absorber. The by-pass was used to supply CO_2 -free air for stirring the titration mixture in the absorber during the final stages of neutralization; the leaf chamber was isolated by taps on both inlet and outlet ports during this time, and so CO_2 accumulated in the leaf chamber as a result of respiration. The subsequent respiration period was therefore always deemed to have commenced at the time that the leaf chamber was isolated and the gas stream diverted through the by-pass. At the beginning and end of each day's experiments the leaf chamber was assembled and connected up without a leaf enclosed, and a set of three blank determinations made over 15 min. periods. The blank determinations for any one day seldom showed any appreciable discrepancy, and were used as a basis for calculating the day's results; the blank value was normally of the order of 0.01 c.c. of CO_2 per hour, except for the initial 15 min. period which gave anything up to 0.1 c.c. of CO_2 per hour, depending on the CO_2 content of the laboratory air (which is enclosed in the leaf chamber).

The CO_2 emitted in respiration was absorbed in baryta solution (approx. 0.03 *N*) in a special type of absorber (Fig. 1) similar to those described by Newton (1935). These absorbers would work efficiently with 5 or 3 c.c. of baryta respectively, but could be made to work with 3 or 4 times that volume of solution if the amount of CO_2 to be absorbed was sufficient to make this necessary. In no case was the normality of the baryta solution reduced to one-half or less through the absorption of CO_2 , and only very rarely was more than one-quarter of the baryta changed into carbonate during absorption. The absorption of CO_2 was estimated by titration with standard HCl of strength approx. 0.005 *N*, using a mixture of phenolphthalein and thymolphthalein as indicator. The delivery jets for all three solutions (automatic pipette for baryta, and burettes for HCl and for indicator) were led into the absorber through a rubber bung which closed the top of the titration chamber, so that the titration could be performed without admitting CO_2 from the laboratory air. During the titration, which usually took about 1 min., the gas flow through the leaf chamber was stopped and the CO_2 -free air which was normally passed into the leaf chamber was brought direct to the absorber through the by-pass. The circulation of solution in the absorber brought about by the continued passage of this air was sufficient to ensure adequate stirring of the titration mixture, and, in fact, made an exact and rapid approach to the end-point extremely easy.

In order to ensure complete absorption of CO_2 the absorption tube (Fig. 1) of the absorber had to be of considerable length, and a zigzag shape was adopted to accommodate this length of tube in the distance between the air inlet and the titration chamber. The length of the return tube from titration chamber to air inlet is governed by the head of pressure required to oppose the suction required to maintain a given rate of bubbling up the absorption tube against the friction and viscosity drag generated in the considerable length of this tube, which is of semi-capillary bore. In addition, the U-tube portion below the air inlet has to be of sufficient length to ensure that the bubbles do not take the path of least frictional resistance and pass up the return tube instead of the absorbing tube.

In order to confirm the reliability of this method of estimation of CO_2 emission over the whole range of respiration rates which would be likely to occur, known amounts of CO_2 were introduced into the air stream and subsequently estimated. The procedure

adopted was to drop a known volume of standard Na_2CO_3 solution from a microburette into a bottle of concentrated sulphuric acid through which the stream of CO_2 -free air was passed before passing through the absorber. The results are shown in Table 1, and

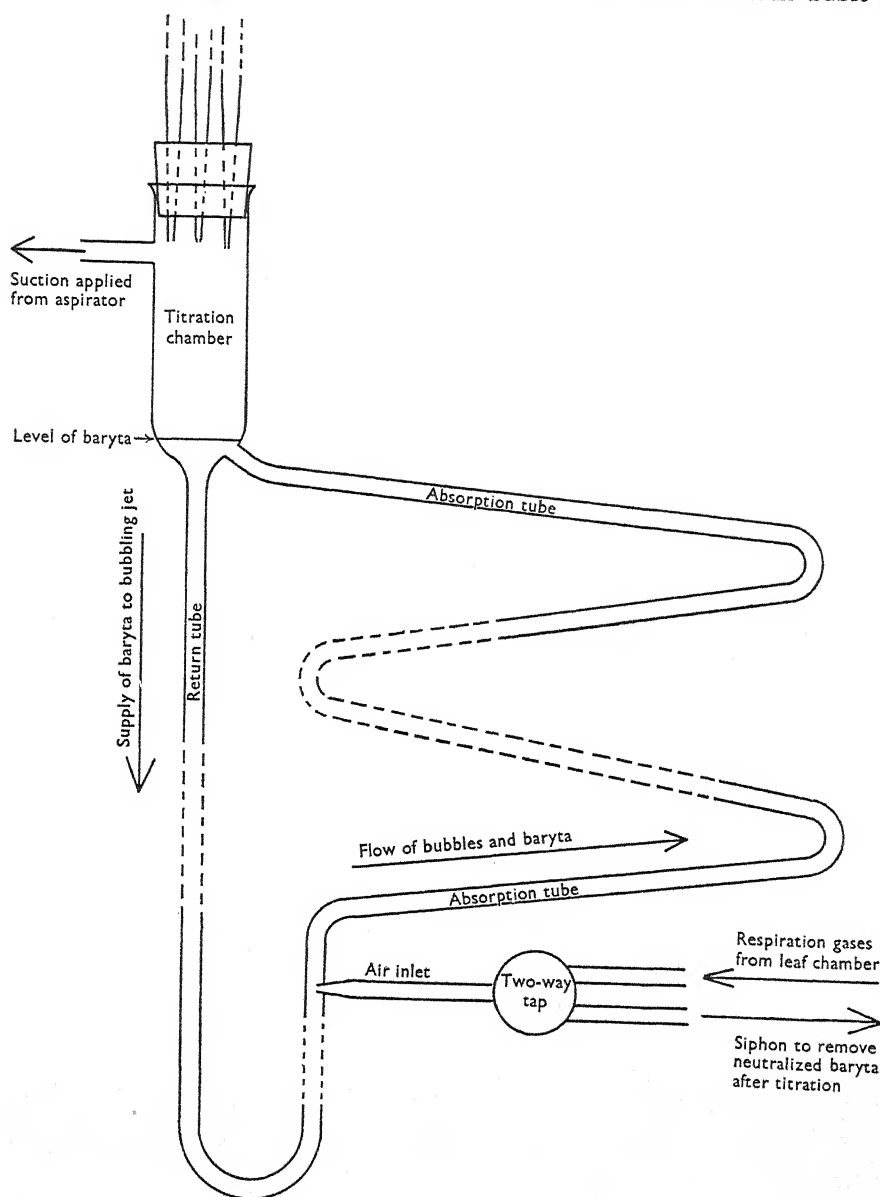


Fig. 1. CO_2 absorption apparatus: the rubber bung is pierced by jets of automatic pipette for baryta, automatic burette for HCl and dropper for indicator.

indicate a positive bias (over-estimation) of 0.006 c.c. of CO_2 and a standard error of 0.013 c.c. of CO_2 ; this is less than 5% of the smallest quantities estimated, and approximately 2% of the amounts more usually encountered in experiments with leaves. The accuracy of the titration itself was determined from fourteen successive estimates of the

volume of standard HCl required to neutralize single shots of baryta from the automatic pipette in the smaller absorber. This gave a standard error of 0.0025 c.c. of CO_2 , which is well below the limit required.

Figures quoted in §§ 3-6 for respiratory activity are always the mean value for the second and third 15 min. periods; the reasons for selecting these two periods are given in § 3. The value assigned to respiratory activity on each particular occasion is, therefore, the mean of two successive determinations on a single leaf which together cover the period from 15 to 45 min. after darkening. The two determinations usually agreed very

Table 1. *Accuracy of estimation of carbon dioxide. Comparison of estimated CO_2 and actual amount supplied*

Carbon dioxide supplied		Carbon dioxide estimated by titration (in c.c. CO_2)
Amount (in c.c.)	Rate (in c.c./hr.)	
0.144	0.30	0.133
0.161	0.48	0.183
0.145	0.29	0.131
0.104	0.36	0.179
0.241	0.34	0.245
0.239	0.49	0.263
0.258	0.55	0.248
0.152	0.32	0.163
0.160	0.34	0.186
0.267	0.59	0.265
0.351	0.84	0.339
0.175	0.39	0.193
0.237	0.53	0.246
0.248	0.60	0.258
0.265	0.55	0.265
0.426	0.88	0.424
0.158	0.34	0.166
0.321	0.71	0.315
0.167	0.40	0.173
0.455	0.98	0.460
0.173	0.40	0.179
0.527	1.22	0.531
0.246	0.55	0.256
0.182	0.64	0.205
0.158	0.35	0.159
0.613	1.47	0.597
0.217	0.52	0.222
0.170	0.36	0.169
0.177	0.39	0.190
0.380	1.50	0.398
Standard deviation		0.013
Bias		0.006

closely with one another; on the few occasions when one determination was very different from the other, the value which corresponded more closely with the initial 15 min. darkness was taken instead of the mean.

The leaf chamber. Two leaf chambers were used, one for fully expanded leaves, and one for young leaves which were still expanding; both were specially designed to be rapidly assembled and sealed, and to contain the minimum volume of air possible without bending or folding the leaflets.

The chamber for expanded leaves consisted of a shallow brass base-plate 8 in. in diameter and 0.4 in. thick, hollowed out on one side to a depth of 0.2 in. over a circular

area 7 in. in diameter (see Fig. 2). A brass 'lid' plate 8 in. in diameter could be fastened over this hollow in the base-plate by means of six screws threaded into holes in the rim of the base-plate. Inlet and outlet tubes were also tapped into the base-plate, and entered the hollow at opposite sides. A rubber sheeting gasket was glued on to the lid with marine glue, and this gasket was renewed from time to time when it failed to make a watertight joint with the rim of the base-plate. Thus, when the lid and base-plate were bolted together there was a small circular space enclosed between them which was approximately 7 in. in diameter and 0.2 in. thick, but the actual capacity of the chamber

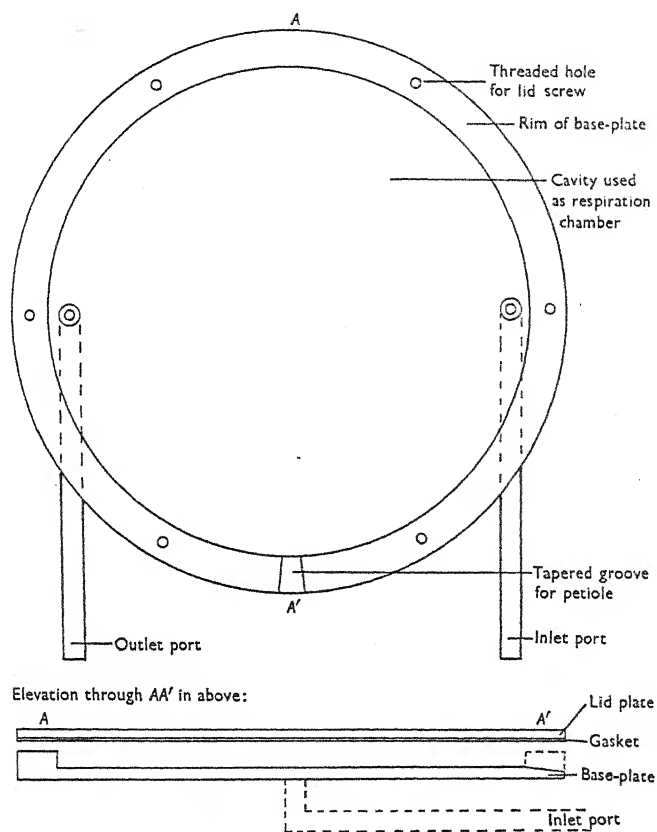


Fig. 2. Leaf chamber with lid removed (base-plate).

could be adapted to the different sizes of leaves at different seasons of the year by partially filling it up with paraffin wax. Paraffin wax was also used to construct internal air ducts from the internal openings of the inlet and outlet tubes, to ensure that there were no dead spaces of still air during operation. The total internal volume of the leaf chamber could be varied in this way from about 50 to about 150 c.c., according to the size of the leaf to be used. A rate of flow of approximately 1 l./hr. was used, and this appears to have been adequate for the removal of CO_2 , since, in nearly all cases, the measured rate of CO_2 emission during the third period of each determination was less than that during the second period.

The petiole of the leaf was accommodated in a slot cut through the rim of the base-plate of the leaf chamber; this slot tapered inwards, and, after assembly of the base-plate and lid, with the petiole in position in the slot, some cotton-wool soaked in vaseline was gently rammed into the slot all round the petiole. The tapering of the slot compressed the reinforced vaseline around the petiole and made an airtight joint. To make doubly certain that the joint was airtight the leaf chamber was usually immersed in the water of the water-bath deeply enough to cover this joint with water.

The leaf chamber used for unexpanded leaves consisted essentially of a small bag made from sheet rubber. Inlet and outlet tubes passed through a rubber bung which was just large enough to close the mouth of the rubber sheeting bag. A small groove was cut down one side of the rubber bung to accommodate the petiole, and a kind of gooseneck made from a strip of sheet brass was used to clamp the mouth of the bag tightly round the rubber bung. The groove in the rubber bung was filled with vaseline, and then the petiole was pressed into the groove with the leaf lamina in position between the open ends of the inlet and outlet tubes; the rubber bag was then put on over leaf and inlet and outlet tubes and rubber bung, and the gooseneck clamped round. In this way an airtight joint could be achieved.

Measurement of leaf area. A stand was constructed to hold two pieces of ordinary glass horizontally over an electric-light bulb. The two sheets of glass were placed one on top of the other in this stand, with several projecting pieces of thick wire between them at the edges so that they were held about 0.1 in. apart. The upper sheet of glass was movable, and had a piece of ordinary typing paper pasted on its upper surface to act as a light diffuser, and also to provide a suitable surface for manipulating the planimeter. Each leaflet was inserted separately between the two sheets of glass and its outline (which was very clear in the light of the electric lamp underneath) was traced with a planimeter, whence the area of the leaflet could be determined.

Leaf areas were usually measured towards the end of the experimental period (a few days before the leaf started to die), as this minimized the handling of the leaf during the early stages of the experiment. There is no reason to believe that the area of any particular leaf changes after the initial unfolding and expansion which occupies the first 3 weeks, unless considerable changes in moisture content are encountered (Thoday, 1910). To verify this assumption the area of six leaflets was determined on 29 August, just 29 days after their first appearance, and 8 days after unfolding appeared to be completed, and the area was determined again 80 days later. The areas were as follows:

Leaflet no.	1	2	3	4	5	6
Area on 29 Aug. 1939 (dm. ²)	0.56	0.35	0.21	0.30	0.25	0.25
Area on 17 Nov. 1939 (dm. ²)	0.58	0.36	0.22	0.30	0.25	0.25

3. RESPIRATION IN PROLONGED DARKNESS

The full significance of isolated measurements of respiratory activity can only be appreciated in the light of a knowledge of the way in which the respiration of the leaf changes from the instant of darkening until some long time after the period in which the measurements to be considered were made. Leaves of different ages were enclosed in the respiration chamber (in complete darkness) for periods of from 6 to 12 hr., and readings were taken for each successive 15 min. period. This was done both in the spring and in the autumn, so that the results are representative of the range of physiological

conditions covered by the main series of experiments. The results are shown graphically in Figs. 3 and 4, and show a remarkable uniformity in behaviour for all leaves, although the level of respiratory activity varies considerably. In all cases there is a slight fall in rate of respiration during the first 2 hr. of darkness, and in most cases this slow decline is continued throughout the experimental period. The only leaves to show any considerable change in respiration rate during the first few hours of darkness are the two

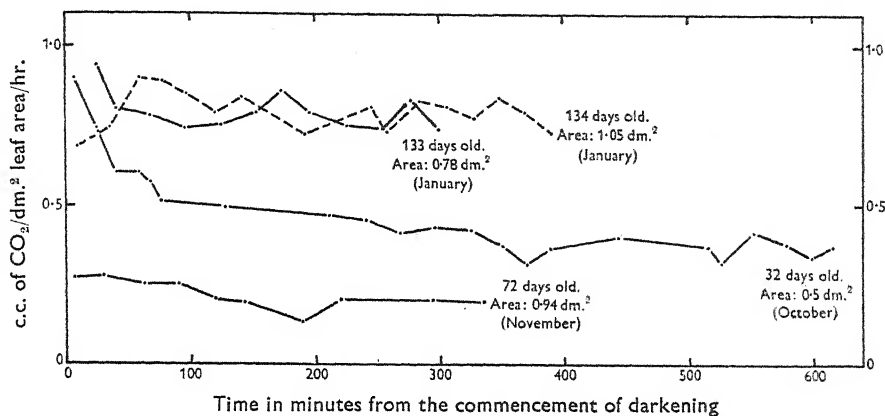


Fig. 3. Respiration of leaves in prolonged darkness during the winter 1939-40.

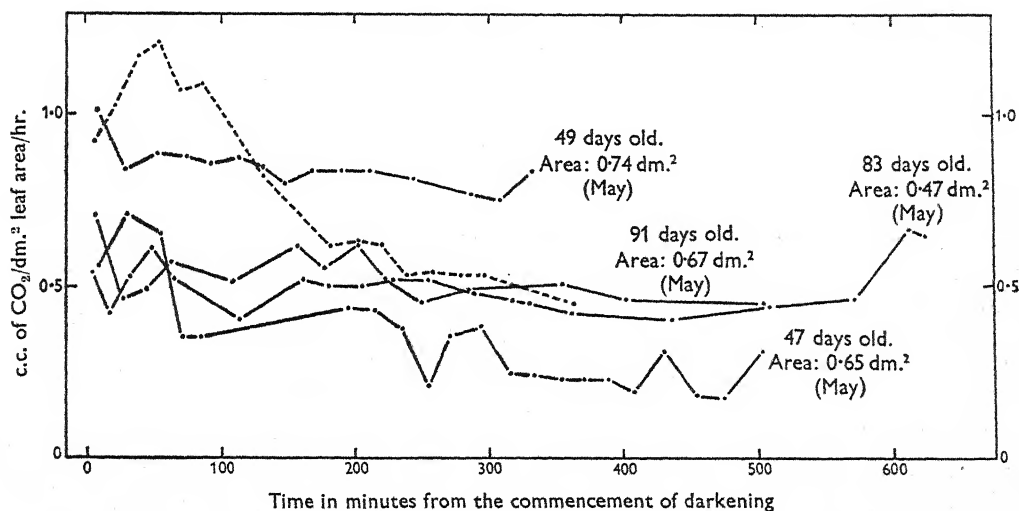


Fig. 4. Respiration of leaves in prolonged darkness during the spring 1940.

young leaves, which both show a high initial rate of respiration; this high initial rate falls rapidly to a much lower level (in one case after rising to a peak value at the end of the first hour). A similar decline in CO_2 emission has been shown for cherry laurel (Godwin & Bishop, 1927), barley and bean leaves (Yemm, 1935), and the slope of the curves for these leaves (judged by extrapolation since the readings were taken at 6- and 11-hourly intervals) appears to be intermediate between the very young expanding leaves, and the older leaves of the strawberry.

The comparatively uniform behaviour of all leaves during the initial 12 hr. after darkening makes it possible to regard the mean CO_2 emission of a leaf over the period from 15 to 45 min. after darkening as a satisfactory and sufficient index of the respiratory activity of that leaf at that particular stage of development. Moreover, this index will apply with equal validity to measurements taken during the day or night, since there is little further decrease in rate of respiration after as long as 12 hr. of darkness. The results seem to indicate, too, that there is very little readjustment in rate of respiration consequent upon the darkening of a photosynthesizing leaf; this agrees with the work of Parija & Saran (1934) in which there was no evidence of any stimulatory effect of exposure of various leaves to light at any time during the first 40 hr. of continuous darkness. This absence of any stimulatory effect of exposure to light is indicated not only by the results of the long-period experiments given in Figs. 3 and 4 but also by the more normal experiments covering the first 45 min. after darkening. In all these experiments the rate of respiration over the first 15 min. after darkening is approximately equal to, and certainly neither consistently greater than, nor consistently less than, the mean rate over the subsequent 30 min., so that there is certainly no very great change in respiration rate during the first hour after darkening.

The form of the curves under consideration for respiration rate during prolonged darkening have an important bearing on the problem of stimulation of respiration through handling the leaves. Audus (1939) has shown that severe handling and bending of the leaves of cherry laurel and other plants induces a very considerable temporary rise in rate of respiration, if this treatment is applied to leaves which have previously been darkened for some hours. This stimulation was demonstrated in all the twenty-two various species used, the increase in respiration varying from 18 to 182% and lasting over a period of 2-3 hr. The general shape of the curves in Figs. 3 and 4 shows conclusively that no comparable stimulation has resulted from the normal manipulation involved in enclosing these strawberry leaves in the respiration chamber. This is only to be expected, since special care was taken not to handle the leaflets more than necessary during the operation of enclosing the leaf in the respiration chamber. A sheet of typing paper was gradually rolled down over the base-plate as the three leaflets were put in place one above the other; this sheet of paper held the leaflets in place while the metal lid was placed in position on the base-plate, and the sheet of paper could then be pulled out from between the lid and the leaf in the base-plate. A further possible reason for the absence of stimulation after enclosure in the leaf chamber is the fact that the leaves of strawberry plants had not been kept in continuous darkness just before manipulation. The stimulation of respiration by mechanical manipulation has only been demonstrated by Audus in leaves detached from the parent plant and kept in continuous darkness for periods of 2 days or more. It is yet to be demonstrated that there is a comparable effect in the case of normal leaves, but it seems unlikely that there is such an effect, except with very severe manipulation, judging from the results obtained with strawberry leaves.

The comparatively slow decline in rate of respiration in continued darkness indicates that the substrate for respiration is present in excess under the conditions of the experiments. That this is so is demonstrated by a further experiment in which detached leaves were kept in a dark room for 24 hr. after the initial respiration determination (consisting of three successive 15 min. periods). At the end of this total period of 24 hr. in darkness a further respiration determination was made and the leaves were then tested for starch

by the usual iodine method. Four leaves from two separate plants were used, and all four leaves had abundant starch in all portions of the leaflets at the end of the experiment, so that there could be no shortage of carbohydrate substrate for respiration unless the starch-sugar equilibrium in these leaves was very abnormal. The respiratory behaviour of these leaves was somewhat irregular; the two leaves from one plant showed a slight *decrease* in respiration over the 24 hr. darkness, while the two leaves from the other plant showed a slight *increase* in respiration. The rates of respiration per dm.² of leaf area of the two 70-day-old leaves were 1.0 and 0.8 at the beginning of the dark period, and 0.9 and 0.97 respectively at the end of the dark period. Corresponding values for two 50-day-old leaves were 0.8 and 0.9 at the beginning, and 0.6 and 1.0 respectively at the end. One may safely conclude, therefore, that both the rate of respiration, and the supply of carbohydrate, are adequately maintained for at least 24 hr. of complete darkness in leaves of this type.

The importance of ensuring that the supply of carbohydrate is adequate in studies on the respiratory capacity of plant tissues has been emphasized by Kidd *et al.* (1921), but applies with equal force in these experiments. A number of leaves of different ages were tested for starch, but no very extensive survey was attempted. The results obtained are summarized in Table 2. It can be seen that starch is rarely present in the *young* leaves until they are considerably past the stage of complete expansion (20 days old), except after a full day's photosynthesis (leaf 10 on plant 2b.3.2a). On the other hand, once the leaf has achieved maturity its starch content remains appreciable, even in the morning, although the absence of photosynthesis during the night, and the activity of translocation, must have reduced the carbohydrate content of the leaf to the minimum at this time. The table also shows that it is only during the period from November to March that starch is absent from the *mature* leaves; towards the end of March starch is found in abundance in all *mature* leaves at the end of a fine day, but this starch has disappeared, presumably as a result of translocation, by the next morning. These results indicate that carbohydrate supply is not limiting the rate of respiration of mature leaves, even after several hours of darkness, at least during the period from April to October, during which a large proportion of the respiration experiments under consideration were done. The *young* expanding leaves probably contain appreciable quantities of starch only after a full day's photosynthesis, and consequently the level of carbohydrate supply for respiration in these leaves is in doubt. In the case of the *mature* leaves during the winter months, the absence of starch may be an indication of absence of carbohydrate in the leaves, or alternatively may be brought about by an alteration in the starch-sugar equilibrium associated with the lower temperatures prevailing during the winter months. The former alternative is more in conformity with evidence to be presented in the next section indicating a tendency for respiration readings to be lower if taken during the morning than afternoon at this time of the year.

The results of earlier researches show that strawberry leaves are not alone in retaining a very considerable proportion of their total carbohydrate throughout the night. The starch content of attached leaves of *Tropaeolum* in the early morning varied from one-quarter to three-quarters of the content in the afternoon (Brown & Morris, 1893); the minimum starch content of mangold leaves, achieved at 0800 hr., was over half the peak value achieved at 1600 hr. (Campbell, 1912); in both cases the concentration of total sugars did not change very much throughout the 24 hr. Miller (1924) found that the

'starch' content (including pentosans) of maize leaves and of *Sorghum* leaves was only reduced to about two-thirds of its maximum daytime value during the night. On the other hand, Davis, Daish & Sawyer (1916) found very little starch left in the leaves of

Table 2. *Starch content of leaves July 1939 to April 1940*

Plant reference no.	Leaf no.	Age of leaf in days	Time of day hr.	Date	Starch content	Remarks
2.1	9	149	2100	July	Dense starch	Large, green
	10	132	1400	July	Dense starch	Large, green
	12	106	1400	July	Dense starch	Large, green
	13	96	1400	July	Dense starch	Large, green
	14	85	1700	July	Dense starch	After day in laboratory
2.2	15	78	1600	July	Dense starch	—
	11	150	—	July	None	Dead and brown
	14	134	—	July	None	Dead and brown
	15	132	—	July	None	Dead and brown
4.1	11	170	—	July	None	Dead and brown
	13	151	—	July	None	Dead and brown
1a	15	144	1400	August	Dense starch	Still green
	16	126	1200	August	Dense starch	Still green
	19	114	1000	August	Dense starch	Still green
	22	99	—	August	Dense starch	Still green
4.3	38	39	—	August	Dense starch	Mature leaf
	16	180	1600	August	Dense starch	—
	17	175	1500	August	in patches Dense starch	—
	18	149	1230	August	Dense starch in green leaflet	—
4.1	50	14	1000	October	None	Half expanded
2b.3.1a	1	32	—	October	Some starch	Fully expanded
	2	22	—	October	Little starch	—
	3	12	—	October	None	Half expanded
3a.1	27	158	1100	October	None	—
	30	148	1100	October	Little starch	—
	40	99	1100	October	None	—
	46	69	1100	October	Much starch	—
4.3	33	150	1300	November	None	—
4.3.2	4	104	1645	November	None	—
	10	51	1230	November	None	—
2b/1a	5	94	1800	December	None	—
2b/2a	5	103	1430	December	None	—
1.1	10	9	1045	1 March	None	—
2.1.2a	3	166	1000	20 March	None	—
	4	148	1000	20 March	Very little starch	—
	6	42	1000	20 March	None	—
	7	37	1000	20 March	None	—
	8	22	1000	20 March	None	—
	9	14	1000	20 March	None	—
	5	184	1800	20 March	Dense starch	—
	6	171	1800	20 March	Some starch	—
1.2.2b	7	151	1800	20 March	Some starch	—
	8	121	1800	20 March	Some starch	—
	9	21	1800	20 March	Little starch	—
	2b.3.2a	6	50	4 April	Dense starch	—
	7	41	1900	4 April	Dense starch	—
	8	30	1900	4 April	Dense starch	—
	9	17	1900	4 April	Dense starch	—
	10	10	1900	4 April	Dense starch	—

the potato at 0200 hr. (about one-tenth of the general level throughout the day). The retention of starch throughout the night in the leaves of the strawberry plant is not unexpected, therefore, especially in view of the absence of any other organs bulky enough to provide appreciable storage space in this plant.

4. EFFECT OF OCCASION, AND OF TIME OF DAY ON RESPIRATION RATE

The successive determinations of respiratory activity on any one leaf fall in a reasonably smooth and well-defined curve, but, as would be expected, readings often depart more or less distinctly from the 'smoothed' curve, and some readings are obviously either very high, or very low, when compared with this 'smoothed' curve. All the readings obtained in all experiments have been assigned to one of five categories which are designated by letters as follows:

H. Readings which are undoubtedly higher than would be expected from the general run of the curve for the leaf in question, and of other curves for similar leaves.

L. Readings undoubtedly lower than would be expected from the general run of the curve for the leaf in question, and of other curves for similar leaves.

h. Readings which are slightly high, or not undoubtedly high.

l. Readings which are slightly low, or not undoubtedly low.

N. Readings falling very near the smoothed curve.

A number of readings, particularly at the beginning and end of each curve, could not be classified with any degree of certainty, and were omitted altogether from this analysis.

Table 3. *Respiratory activity at different times of the day. Total numbers of 'High' (H), 'Normal' (N), and 'Low' (L) readings obtained during different portions of the day*

Date	1000-1200 hr.			1200-1500 hr.			1500-1800 hr.			1800 hr. onwards		
	H	N	L	H	N	L	H	N	L	H	N	L
Aug.-Dec. 1939	1	9	4	7	17	7	6	9	10	2	3	1
Feb.-Mar. 1940	2	9	10	1	4	5	5	8	9	0	0	0
Apr. 1940	6	8	4	4	12	0	7	31	6	0	3	2
May 1940	5	7	2	3	4	2	4	2	1	0	0	0
June-Sept. 1940	3	14	7	9	23	9	4	8	5	0	0	0
Total	17	47	27	24	60	23	26	58	31	2	6	3

Table 4. *Respiratory activity on different days. Distribution of readings of each type*

Date	No. of days of each type			Total no. of readings of each type					Total no. of readings obtained on normal days				Total no. of readings obtained on H and L days			
	H	N	L	H	h	N	L	l	H	h	L	l	H	h	L	l
Aug.-Dec. 1939	3	13	5	7	12	48	21	11	2	8	9	7	5	4	12	4
Feb.-Mar. 1940	1	8	4	3	7	19	19	3	4	4	10	1	0	3	9	2
Apr. 1940	1	12	0	10	6	53	4	10	7	6	4	10	3	0	0	0
May 1940	2	5	1	5	7	15	3	2	2	5	1	2	3	2	2	0
June-Sept. 1940	2	13	3	9	7	36	7	9	4	6	3	5	5	1	4	4
Total	9	51	13	34	39	171	54	35	19	29	27	25	16	10	27	10

Table 3 shows the numbers of readings of each of the three definite categories (*H*, *N*, *L*) which were obtained at different times during the day. It can be seen that, in general, the time of day at which the experiment is carried out has little effect on the rate of respiration. In the autumn and winter months, however, there is a slight tendency

towards low readings before noon; this is probably the effect of the long dark period to which all plants are naturally subjected during the long winter nights. The possibility of an insufficient supply of carbohydrate at this season is considered in § 3.

Tables 5-7 give the distribution of all classified readings on those days on which measurements were made on three or more different leaves. On the basis of these data each day included in the tables has been classified as a 'high', 'low', or 'normal' day as regards respiratory activity. Days were only considered to be 'high' if there were no undoubtedly low readings on that day, and if 50% or more of all readings for the day were high; a comparable standard was used to allocate 'low' days, and all other days were considered as 'normal'. The analysis of these results in Table 4 shows that just under 70% of all days included in the analysis were 'normal' days, and that less than 50% of all *H* or *L* readings occurred on high or low days. Many of the irregularities in respiration rate are not therefore attributable to those factors of the environment which are uniform throughout the greenhouse but may vary from day to day, such as the climate; these variations in rate of respiration must therefore be attributed to factors of the environment which are peculiar to the individual leaves, or to their physiological condition.

The shade temperature in the greenhouse, and the general weather conditions associated with the 'high' and 'low' days, are given in Table 8. There is little connexion between the recorded conditions, either of temperature or of sunshine, on the day of the experiment and the sense of the abnormality of the readings on that day, but previous weather seems to have some influence, and there is a distinct tendency for 'low' days to follow a period of dull weather. Both this analysis, therefore, and the absence of any marked effect of time of day on rate of respiration, point to the conclusion that the environment of the plant immediately before the measurement of respiration has little effect on the rate of respiration of the leaf under standard conditions. Otherwise the time of day would be expected to show a marked effect since the temperature in the greenhouse is much higher between 1400 and 1600 hr. than at other times, and one would expect the light intensity to be higher during the noontide hours, especially during the winter months.

5. CHANGES IN RATE OF RESPIRATION ASSOCIATED WITH AGEING OF THE LEAF

Successive determinations of the rate of respiration on one and the same leaf at frequent intervals show a general drift in respiratory activity (Figs. 5-9) which is essentially the same in all the leaves investigated except the 'summer' leaves which expand in April, May, and June; the latter will be considered at the end of this section. While the leaf is unfolding and expanding, the rate of respiration of the leaf increases rapidly, and achieves its maximum value at, or just before, unfolding is completed (10-15 days after emergence of the leaf). This rapid rise in rate of respiration seems to be already fully operative at the youngest stages ever used in experiments—5 days after emergence. It is followed by an almost equally rapid fall in respiration rate to the general level characteristic of the adult leaf, which is usually achieved before the 20th day after emergence. From this time until well after 100 days after emergence the rate of respiration remains relatively constant, with only a very slight, though definite and continuous, decline with increasing age of the leaf. This period of slowly declining respiration rate terminates in

Table 5. Respiratory activity on different days. Assignment of readings on each day for the period August-December 1939, to various categories

H = undoubtedly high. h = possibly high. N = normal. L = undoubtedly low. l = possibly low.

Date	Reference no. of leaf												Total no. of readings of each type					'Type of day		
	1.3/46	1.3/47	1.3/45	1.3/49	2.1/45	2.1/46	2b.2a/5	2b.2aa/3	2b.3/6	2b.3a/4	4/55	4/54	2.2/45	H	h	N	L		l	
11 Aug.					2	1	1	.	.	1	High
18 Aug.	7	II	H	H	1	1	1	3	1	1	Normal
25 Aug.			2	1	.	Normal
27 Sept.			5	2	.	Low?
28 Sept.			2	4	.	Normal
29 Sept.			2	1	.	Low
30 Sept.			3	4	.	Normal
2 Oct.	H	1	2	2	2	1	1	Normal
3 Oct.	2	2	.	Normal
4 Oct.	1	2	.	Normal
7 Oct.	2	1	.	Normal
9 Oct.	4	1	.	Normal
10 Oct.	2	.	.	Normal
17 Oct.	3	.	.	Normal
26 Oct.	2	1	.	Low?
9 Nov.	2	3	1	Low
21 Nov.	2	1	1	4	2	2	Normal
30 Nov.	3	.	.	High
1 Dec.	4	1	.	Normal
14 Dec.	1	2	1	Low
28 Dec.	2	2	.	.	High
														7	12	48	21	11	3H, 13N, 5L	

Table 6. Respiratory activity on different days (as Table 5), for the period February-May 1940

[illegible]

Table 7. Respiratory activity on different days (as Tables 5 and 6), for the period June-September 1940

Date	Reference no. of leaf										Total no. of readings of each type					Type of day	
	4-1/18	4-2/17	26-1/20	26-1/21	26-1/22	1-2-1a/15	1-2-1a/16	26-3-1/18	4-1-1a/22	4-3-1a/22	2-2-1/27	H	h	N	L		I
6 June	N	.	.	.	N	3	.	1	Normal
8 June	N	.	.	.	N	1	.	2	Low?
10 June	N	.	.	.	N	1	3	1	Low
14 June	N	.	.	.	N	1	.	1	Normal
17 June	N	.	.	.	N	2	.	1	Normal
18 June	N	.	.	.	N	1	1	1	Normal
22 June	N	.	.	.	N	2	.	1	Normal
2 July	N	.	.	.	N	1	.	1	High
8 July	N	.	.	.	N	2	.	1	High
13 July	N	.	.	.	N	1	.	1	Normal
19 July	N	.	.	.	N	3	.	1	Normal
22 July	N	.	.	.	N	2	1	1	Normal
31 July	N	.	.	.	N	2	1	1	Low?
5 Aug.	N	.	.	.	N	3	.	1	Normal
14 Aug.	N	.	.	.	N	3	.	1	Normal
19 Aug.	N	.	.	.	N	4	.	1	Normal
27 Aug.	N	.	.	.	N	3	.	1	Normal
3 Sept.	N	.	.	.	N	2	.	1	Normal
												9	7	36	7	9	2H, 13N, 3L

a more or less marked rise in respiration which usually occurs simultaneously with the yellowing of the leaf at the beginning of its death.

The general trend in respiration rate of leaves with age has also been demonstrated by quite a different method, and the results (Figs. 10, 11) agree well with the above account. The curves shown in Figs. 10 and 11 were obtained by measuring the rate of respiration of each successive leaf on one particular plant; these leaves will be of various ages ranging from young to dying leaves, so that the results can be plotted to show the variation in rate of respiration per unit leaf area ('Respiratory activity') with age of the leaf, from expansion to death (Figs. 10, 11).

Table 8. *Respiratory activity, temperature, and weather. Temperature and weather all days on which respiratory activity was abnormally high or low for August 1939 to July 1940*

Date	Respiratory activity	Temperature °C.		Weather for day	Weather during previous days
		Min.	Max.		
11 Aug.	High	—	18	Little sun	Several dull days
27 Sept.	Low?	10	21	Little sun	Several dull days
29 Sept.	Low	10	23	Some sun	Several dull days
10 Oct.	Low?	13	19	Dull	Two very dull days
17 Oct.	Low	9	11	Very dull	Several very dull days
9 Nov.	High	15	21	Some sun	Warm dull days
1 Dec.	Low	13	13	Dull	Warm, very dull days
14 Dec.	High	9	9	Dull	Dull cool days
28 Feb.	Low	13	16	Dull	Little sun; warm days
2 Mar.	Low	10	27	Sunny	1 March sunny; previous days cold and dull
12 Mar.	High	12	14	Dull	Very sunny week
13 Mar.	Low	13	19	Some sun	See 12 March
18 Mar.	Low	13	21	Some sun	Two dull days
16 Apr.	High?	10	24	Some sun	Two very sunny days
30 Apr.	High	15	20	Some sun	Not known
8 May	Low?	15	29	Sunny	Five hot sunny days
13 May	High	12	29	Sunny	Very warm sunny week
29 May	High	—	—	Sunny	Hot sunny days
8 June	Low	16	35	Sunny	Very hot sunny week
10 June	Low	18	26	Some sun	Very hot sunny week
2 July	High	—	34	Sunny	Very hot sunny days
8 July	High	—	34	Sunny	Very hot sunny week
31 July	Low?	18	35	Sunny	30 July cool and cloudy, after hot sunny week

These results are of interest, not only because they corroborate the evidence obtained from successive determinations on one and the same leaf at different times, but also because they show clearly the relation between rate of respiration of the leaf and area of the leaf. Successive leaves on the same plant often vary considerably (as much as 50–100% in area), and in rate of respiration, but when the rate of respiration is corrected for differences in leaf area the resultant values for the 'respiratory activity' of adjacent leaves on the plant are very similar, as shown by the comparatively smooth curves obtained (Figs. 10, 11). The same relationship between rate of respiration and leaf area is shown in all the other leaves used for other types of experiment; the actual rates of respiration and leaf areas of the various leaves are often widely different, but the rates of respiration *per unit leaf area* for comparable ages and comparable leaves are very

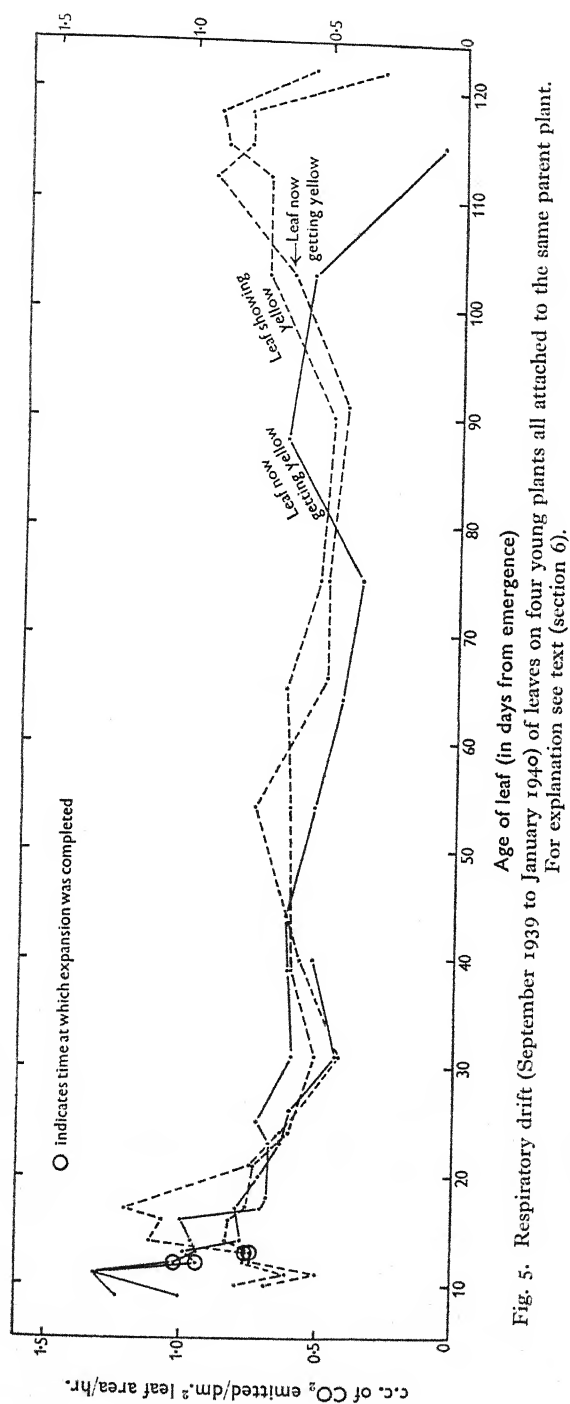


Fig. 5. Respiratory drift (September 1939 to January 1940) of leaves on four young plants all attached to the same parent plant. For explanation see text (section 6).

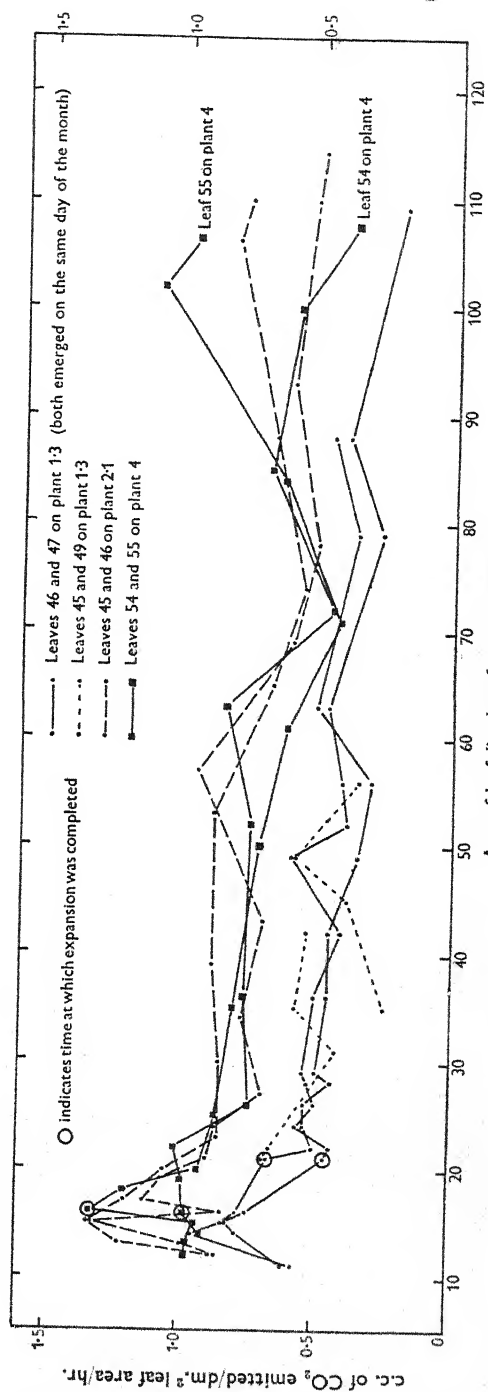


Fig. 6. Respiratory drift (August to December 1939) of leaves on 12 months' old plants (leaf 54 emerged one day before leaf 55; hence readings taken on the same day of the month on these two leaves are plotted one day apart on the graph).

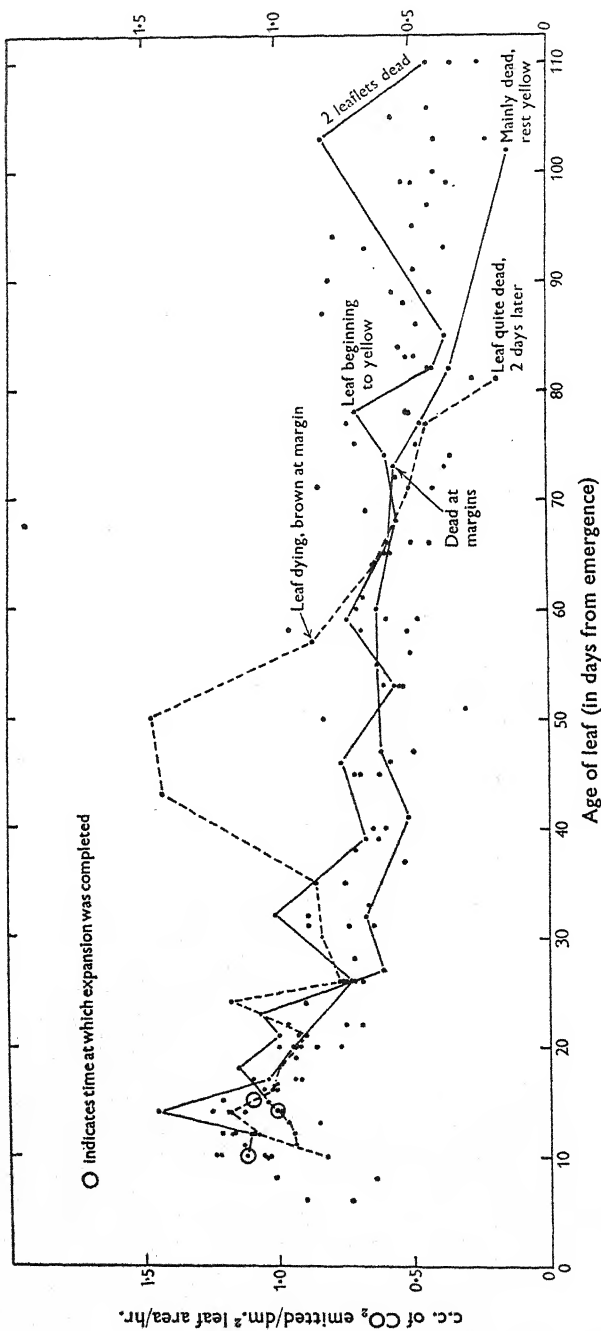


Fig. 7. Respiratory drift (March to July 1940) of leaves of young (6 months) plants. A few typical curves have been drawn; the points for other leaves are left disconnected to avoid confusion of lines.

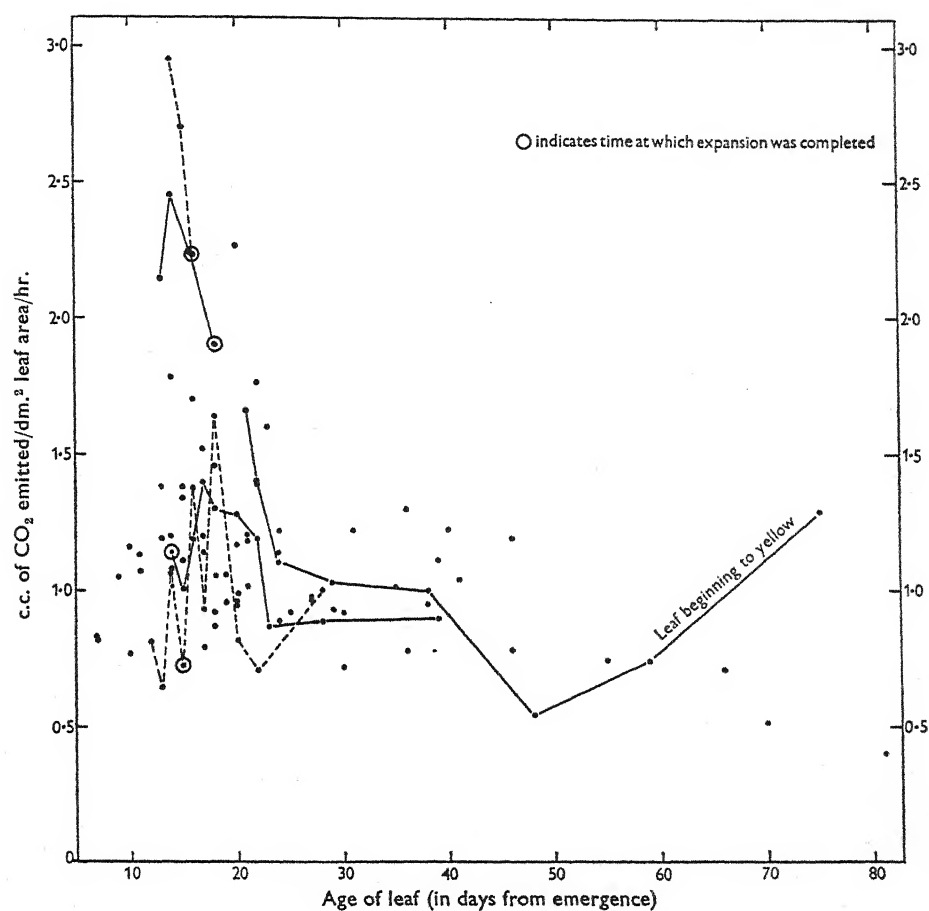


Fig. 8. Respiratory drift (March to June 1940) of leaves on old (18 months) plants. A few typical curves have been drawn; the points for other leaves are left disconnected to avoid confusion of lines.

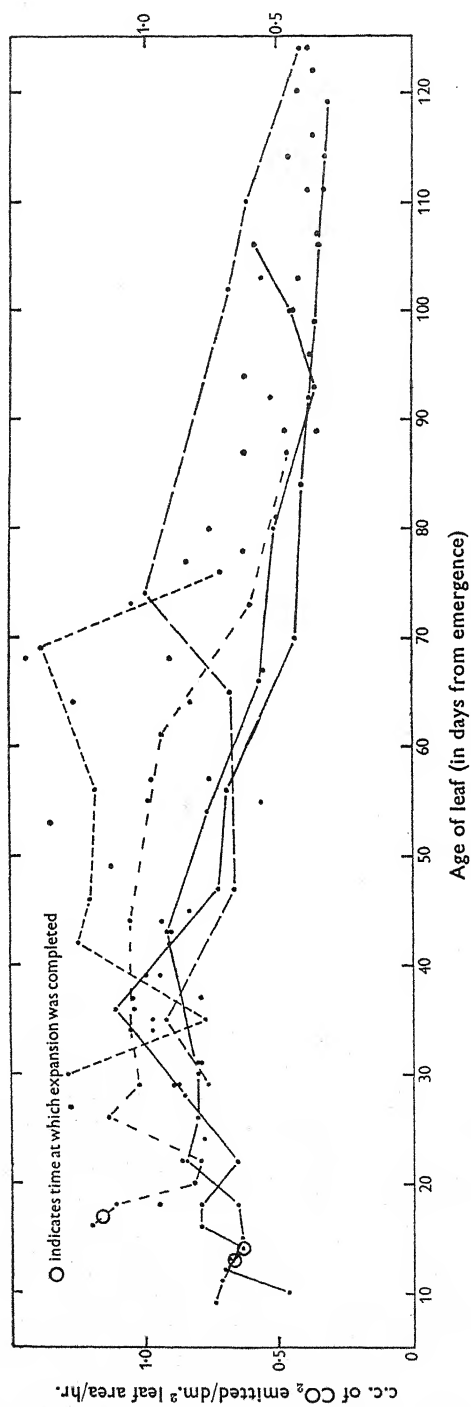


Fig. 9. Respiratory drift (June to October 1940) of leaves on old (12 months) plants. A few typical curves have been drawn; points for other leaves have been left disconnected to avoid confusion of lines.

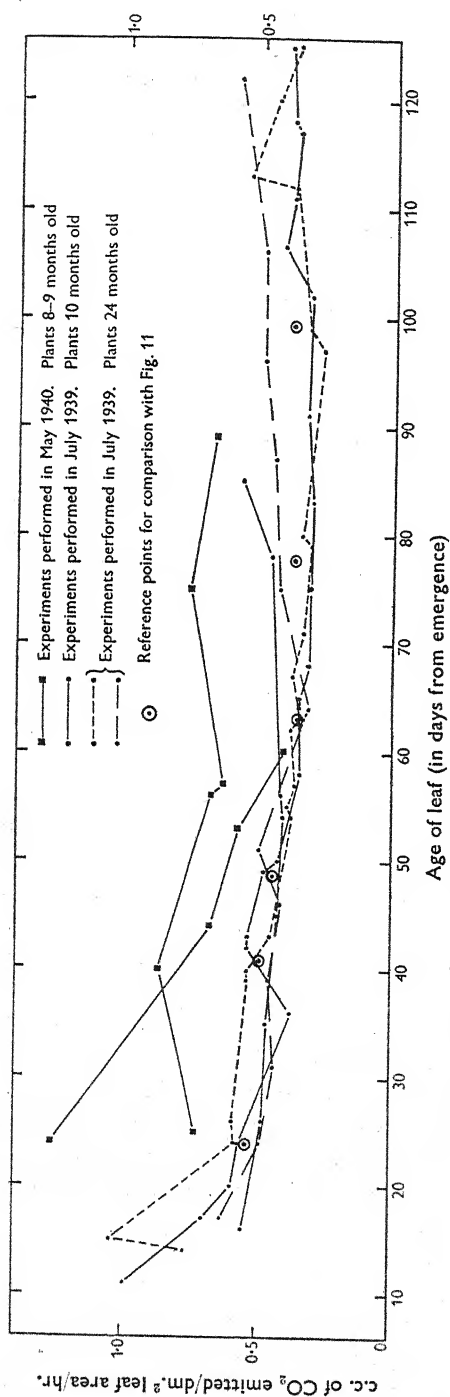


Fig. 10. Respiratory activity of successive leaves on individual plants (May and July).

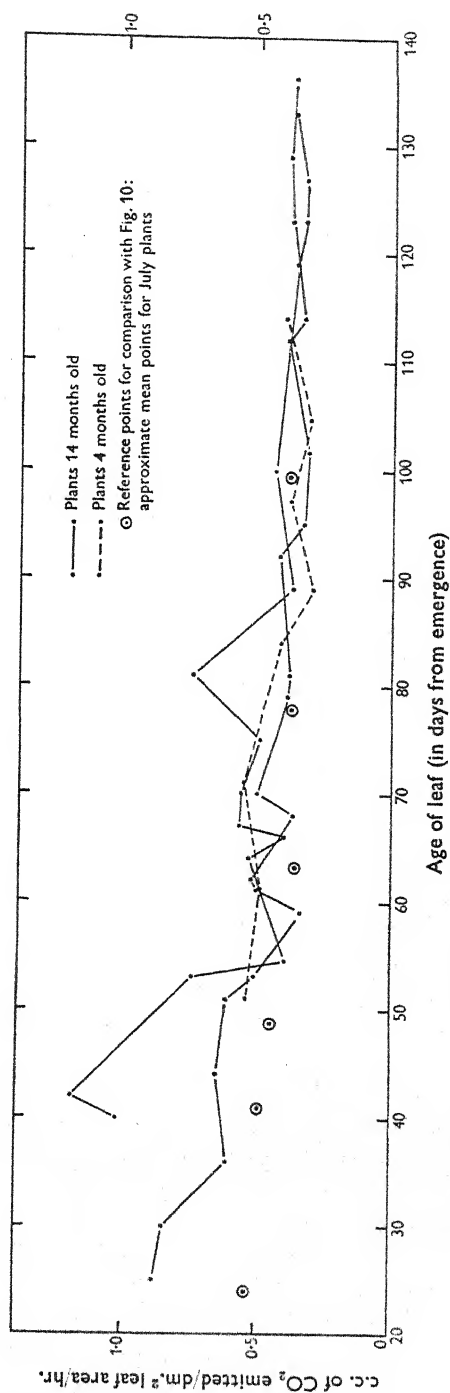


Fig. 11. Respiratory activity of successive leaves on individual plants (October to November 1939).

similar (Figs. 5-9). The respiratory activity is therefore a very useful basis for comparing the rate of respiration of different leaves; in addition, it has the advantage that curves for respiratory activity of individual leaves have exactly the same shape as curves for rate of respiration throughout the life of the leaf. This follows from the fact that the leaf area has been shown not to change appreciably during the adult life of the leaf (§ 2), so that one particular value for leaf area can be used for all the respiration determinations on any one particular leaf throughout its life.

The earliest stage at which respiration determinations were ever made was during the period of rapid vacuolation of the cells resulting in expansion and unfolding of the leaves. By this time all meristematic activity has ceased in the leaf (Priestley and Scott, 1938), with the possible exception of the intrafascicular cambium of the main veins, which is a very small proportion of the total number of cells in the leaf. It seems fairly certain, therefore, that the number of cells in any one leaf did not change appreciably during the whole period of the respiration readings, from expansion to death. Moreover, these cells are predominantly of a comparatively unspecialized nature, belonging to the mesophyll and palisade tissues of the leaf; the epidermis and the phloem are the only other two types of living (and therefore respiring) cells which are present in appreciable numbers. From the point of view of respiratory activity, therefore, each leaf can be regarded as an aggregation of cells similar in origin and in age, and predominantly similar in type. This is relevant in connexion with the considerations brought forward in subsequent paragraphs.

If we regard each leaf as an aggregate of cells identical in origin, age, and type, and invariable in number in any one leaf, then the drift of respiratory intensity of a leaf can also be taken to indicate the drift in respiratory activity with age of the typical protoplast from the main type of cell in that leaf. If we assume similar cell dimensions for comparable cells in different leaves, then the ratio of respiratory activities (=respiration per unit leaf area) of any two leaves also gives the ratio of respiratory activities of single protoplasts from these two leaves. Again, a change in respiration rate of any particular leaf indicates either a change in the amount of protoplasm in each protoplast, or a change in the respiratory activity of the (constant) amount of protoplasm in the protoplast, or a combination of both; it has been shown in § 3 that the amount of carbohydrate substrate of respiration was not limiting in any of these experiments.

In the light of these considerations the rapid increase in rate of respiration during expansion of the leaf is somewhat unexpected. The number of cells in the leaf is not increasing, and it does not seem reasonable to suppose that the amount of protoplasm in each protoplast undergoes a similar rapid increase and subsequent decrease. Again, the maximum respiratory activity appears to occur just as vacuolation is being completed, and not in the middle of the vacuolation period as would be expected if the increase in respiration were associated with the process of vacuolation.

The definite rise in rate of respiration which is associated with yellowing and death of the leaf is of considerable interest, since a similar phenomenon was demonstrated by F. F. Blackman (1908) during the yellowing of *detached*, darkened leaves. This 'yellowing rise' was not demonstrated in all experiments on attached normal leaves of strawberry, but, apart from the 'summer leaves' mentioned later, out of the twenty-seven leaves which were under observation during senescence, twenty-two showed some appreciable rise in respiratory activity at this time (Table 9). Of the twenty-two leaves which showed

a 'yellowing rise' seventeen were noted as showing signs of impending death at the same time, and one was completely dead 5 days after the rise without showing previous signs of death. (Leaves normally went yellow at this stage, but some started to wither and go brown and dry without first going yellow.) Those leaves for which no 'yellowing rise' is recorded may quite possibly have passed through this stage unnoticed, as readings

Table 9. *Respiration and yellowing of leaves July 1939 to May 1940*

The maximum values of respiratory activity at the peaks coinciding with: A, complete expansion of the lamina; D, the onset of yellowing. Also the limits of drift in respiratory activity during adult life: B, at the end of the rapid fall after expansion is completed; C, just before the 'yellowing rise'. The age of the leaf when yellowing commenced, and when the 'yellowing rise' was first detected, and the condition of the leaf when this rise was detected. The leaves on each plant are numbered successively from 1 as they arise; the leaf number therefore indicates the age of the plant on which it is borne. Leaves on same plant are bracketed.

Leaf no.	Date of emergence of leaf	Respiratory activity				Age of leaf at (days)		Condition of leaf at time of yellowing rise
		A	B	C	D	Yellowing	Yellowing rise	
43}	28 July	—	—	0.3	0.6	125	143	Quite yellow
45}	31 July	—	—	0.3	0.68	122	140	Fairly yellow
46}	31 July	0.83	0.5	0.3	0.51	—	63	Unknown
47}	31 July	0.95	0.5	0.4	0.57	126	136	Fairly yellow
45}	12 Sept.	1.33	0.7	0.7	0.95	101	57	Normal; green
46}	17 Sept.	1.32	0.8	0.6	0.82	97	106	Slightly yellow
54}	21 Sept.	1.02	0.8	0.4	0.69	—	85	Unknown
55}	22 Sept.	1.33	0.9	0.4	1.1	95	102	Hardly yellow
5	16 Sept.	0.84	0.5	0.5	0.92	103	103	Just yellowing
3	16 Sept.	1.2	0.5	0.4	0.93	91	103	Just yellowing
6	16 Sept.	1.3	0.7	0.4	0.65	88	88	Just yellowing
4	11 Sept.	—	—	0.5	0.74	116	116	Just yellowing
71}	2 Feb.	1.7	1.1	0.5	1.3	75	75	Just yellowing
75}	7 Feb.	1.2	1.0	0.4	None	70	None	No rise
76}	20 Feb.	1.2	0.7	0.5	None	65	None	No rise
14}	27 Feb.	—	—	0.5	0.8	90	90	Browning
15}	15 Mar.	1.1	0.8	0.5	1.94	55	65	Yellow and brown
12	15 Mar.	1.2	0.8	0.4	None	59	None	No rise
14	15 Mar.	1.4	0.8	0.1	None	73	None	No rise
13	10 Mar.	1.2	0.9	0.6	0.84	71	71	Just yellowing
17	14 Mar.	1.1	0.6	0.4	0.83	82	103	Yellow and dead
15	13 Mar.	1.1	0.7	0.5	0.67	82	61	Normal; green
12	15 Mar.	1.2	0.7	0.6	0.7	66	60	Normal; green
15	8 Mar.	—	—	0.5	0.82	87	87	Just yellowing
14}	11 Mar.	1.2	0.8	0.8	1.4	77	43	Browning
15}	23 Mar.	—	—	—	None	93	None	No rise
12	10 Mar.	1.1	0.7	0.5	0.95	—	58	Dead 5 days later
20}	8 May	—	0.8	0.7	1.0	110	74	Normal; green
21}	12 May	—	None	None	0.97	100	37	Normal; green
22}	19 May	—	None	None	0.97	114	34	Normal; green
16	9 May	—	None	None	1.25	68	42	Normal; green
17	10 May	1.3	None	None	1.3	73	43	Normal; green
18	19 May	1.2	None	None	1.1	61	26	Normal; green
18	26 May	0.74	None	None	0.91	80	43	Normal; green
22	27 May	0.8	None	None	1.1	70	36	Normal; green

were only taken at infrequent intervals during the later life of the leaf and the 'yellowing rise' appears often to have been short-lived. The information obtained on these points has been summarized in Table 9 since the graphs in Figs. 5-9 do not always include the 'yellowing rise' (if this occurred later than 120 days after emergence), and also it would be impracticable to draw in all the curves obtained.

The 'summer leaves' which expand in April, May and June are almost double the size of the spring and autumn leaves and have longer, more erect, petioles. Their respiratory activity is much higher throughout life than the smaller leaves, and often continues on through the adult period at the same level as in the period of expansion. Unfortunately only three leaves of this type were under investigation early enough to cover the period of expansion, and their respiratory behaviour during this period was not uniform. Two of the three leaves showed a gradual increase during and after the expansion period (Fig. 9) to a prolonged maximum which lasted almost into the senescent stage. The other leaf showed the usual rapid increase to a maximum at the time of complete expansion, but the subsequent rapid drop was very short-lived, and the respiratory activity during most of the adult period was almost as high as at the time of complete expansion. Other leaves of this type which were used for respiration determinations also confirmed the high rate of respiration during the adult life of the leaf, but no data have been obtained suggesting a reason for this difference between summer leaves and spring and autumn leaves. The absence of any 'yellowing rise' in these summer leaves (see Table 9) is another feature in which their respiratory behaviour differs from leaves produced at other seasons. This characteristic may possibly be related to the fact that none of these leaves showed any signs of yellowing during old age, but all changed colour to a bright red or purple at the time of senescence, and then became brown and withered in the usual way.

6. VARIATIONS IN RESPIRATORY ACTIVITY BETWEEN INDIVIDUAL LEAVES; THE EFFECT OF SEASON, AND AGE OF THE PARENT PLANT

The respiration results are not in a convenient form for an analysis of variance as between individual leaves and individual plants, but it seems likely that variations in respiratory activity of successive leaves on the same plant are appreciably smaller than variations between leaves on different, but comparable, plants. Two main lines of evidence can be considered in this connexion. First, the curves in Figs. 10 and 11 show a tendency to remain distinct from one another (they do not cross and recross) over considerable portions of their length. Any one curve is constructed from the readings obtained on successive leaves from a single plant, so that the difference between groups of successive leaves of comparable ages on different plants is represented by the degree of separation of the curves for these plants. Secondly, the curves in Fig. 6 show clearly how similar are respiratory drifts of adjacent leaves on the same plant in relation to the differences between the drifts of pairs of adjacent leaves on different plants, comparable with each other. The difference between plants 1.3 and 2.1 is particularly striking.

The curves shown in Fig. 5 were obtained from four different leaves on four different, very young, runner plants, all developed from the same parent plant, and still attached to it by a healthy growing runner stem. The two dotted lines represent leaves on two plants developed at successive nodes on one runner stem, and the two solid lines were obtained from leaves on two plants developed at successive nodes on another runner stem from the same parent plant. The similarity between leaves on different plants on the same runner stem is striking, but needs confirmation. These four leaves all emerged on the same day of the month, and variations between curves cannot therefore be ascribed to different external conditions at the time of the determinations. This makes the contrast between

the two pairs of plants on the 8th, 10th and 11th days after emergence of the leaf all the more striking.

In this preliminary survey of the respiratory behaviour of strawberry leaves it was impossible to obtain adequate data for a full and complete comparison of leaves on plants of different ages and at different seasons, but Figs. 5-8 indicate the possibilities.

No fresh leaves emerge on strawberry plants during December and January, unless the plants are wintered in a warm house; only towards the end of February do leaves begin to emerge in quick succession, and a steady rate of emergence of fresh leaves continues from this time onwards until October. The characteristic summer leaves are formed towards the middle of this growing period, and so it seemed reasonable to divide the period into three seasons in the expectation that the leaves emerging in each season might be physiologically distinct. Leaves emerging in February, March and early April are called 'spring' leaves; the 'summer' leaves arise in late April, May and June; the leaves emerging in the last half of July, and onwards into November are called 'autumn' leaves. Since new plants arise from runners in July, August and September, spring leaves will arise on plants which are 6-9 months old, or 18-21 months old, or 30-33 months old, etc.; summer leaves will arise on plants which are 8-11 months old, 20-23 months old, or 32-35 months old, etc.; and autumn leaves will arise on plants which are 1-3 months old, 13-15 months old, or 25-27 months old, etc.

A comparison of Figs. 5-8 shows that there is very little difference between the respiratory behaviour of the spring and autumn leaves. The general trend of the curves for the spring leaves over the first 50 days of life of the leaves is slightly higher than for the autumn leaves, but, considering the scatter of the individual curves in each case, it seems rather unlikely that this difference would be found to be statistically significant. One might expect (see § 4) the general climatic conditions during the early life of the spring leaves used in the experiments (March to July) to induce a somewhat higher general level of respiration than the autumn leaves would show during the experimental period (September to January). The slight differences between spring and autumn leaves shown in Figs. 5-8 may therefore be attributable to the different climatic conditions in the two periods under consideration.

The only marked effect of season on the respiratory activity of leaves is shown by the summer leaves, and in this case other marked differences are also apparent (see § 5). In spite of the wide scatter of points in Fig. 9, it is reasonable to consider that the general trend of respiratory activity in this case is higher than for any other type of leaf, during the period from 20 to 70 days after emergence. The absence of a yellowing rise in respiratory activity in any of these leaves is also in distinct contrast with other types of leaf.

By comparing leaves emerging in the same season on plants of different ages, an indication of the effect of age of the plant is obtained. Such a comparison for autumn and spring leaves is available in Figs. 5 and 6, and Figs. 7 and 8 respectively; unfortunately, there is no similar comparison available for summer leaves. It can be seen that there is no evidence of any appreciable difference in the level of respiratory activity of the leaves on plants of different ages. If we exclude the curves for plant 1.3 from Fig. 6 on the grounds that the plant is perhaps not representative of the general type used for all other experiments, it would be possible to regard the leaves on the older plants as showing a slightly higher rate of respiration during the first 50 days in both spring and autumn,

but this interpretation is not borne out by the results of experiments illustrated in Figs. 8 and 9; in these figures, the curves for plants differing in age by as much as 12 months are absolutely indistinguishable in general level. The whole evidence therefore strongly favours the supposition that the age of the plant has no effect on the general level of respiratory activity of the individual leaves, at least for the first 2 years of life. Unfortunately, the war put a stop to the experiments before older plants of the same clone were available for comparison.

These results, indicating that the age of the plant may have little effect on the respiration of individual leaves is not necessarily in contradiction with the results of Kidd *et al.* (1921) on sunflower plants. They found that the respiratory index (respiration per unit dry weight) of the 'top cluster of leaves' (exact nature unspecified) decreased considerably with age of the plant, but they admit that changes in respiratory index of other portions of the plant are more a function of the chemical content of the organs than of the rate of respiration, and it is difficult to be sure of the precise significance of this respiratory index when applied to the 'top cluster of leaves'; the inclusion or exclusion of the oldest leaf of this cluster might make a considerable difference to the respiratory index. It seems therefore that these variations in respiratory index do not necessarily indicate variations in the actual respiratory activity of the protoplasts of the apical meristems.

Singh (1935) claims to have shown that the respiratory index (respiration per unit dry weight) of apical meristems of a large number of species investigated by him decreases with age of the plant, and that the long-lived species show a higher initial respiratory index, and a slower ontogenetic decline in respiratory index than the short-lived species. The experimental data on which these conclusions are based are not given, however, and there is no indication of the methods used for 'the selection of only that region of the meristem which is free from non-living tissues...', and in the absence of more explicit information on these points it is difficult to assess the significance of the conclusions drawn by the author. The meristems were kept in the laboratory for 20 hr. after excision before respiration was measured so that one might expect the meristematic tissue to be in an advanced stage of carbohydrate starvation during the respiration determinations, and consequently differences in respiratory index between different species may merely reflect the different degrees of starvation induced by the pretreatment.

It appears, therefore, that there is still no reliable evidence indicating a change in respiratory activity of the protoplasm of plants with increasing age of the individual plant, and the absence of any detectable difference in the respiratory activity of the leaves on strawberry plants of different ages is not entirely unexpected.

7. SUMMARY

Successive determinations of the respiration of individual strawberry leaves over 15 min. periods have been obtained by measuring the CO_2 emission of single darkened leaves while they remained attached to the plant. Special absorption apparatus and leaf chambers are described in which the standard error of a single titration is equivalent to 0.0025 c.c. of CO_2 , and the standard error of a single determination of CO_2 absorbed from a gas stream of approximately 1 l./hr. passing from 0.3 to 1.5 c.c. of CO_2 /hr. is not more than 0.013 c.c. of CO_2 .

Individual leaves attached to the plant were kept in darkness at 24.5°C . for periods up to 10 hr., during which respiration determinations were made every 15 min. Short-period fluctuations in rate of respiration during these experiments were remarkably small. In general, there is a slight initial decline in rate of respiration, but after about 3 hr. darkness the rate does not change appreciably up to the termination of the experimental period, except in the case of young, partially expanded leaves, which show a more marked and more prolonged decline in respiration rate.

It is shown that there is abundant starch in all leaves except the young expanding leaves, even after 12 hr. or more of continuous darkness, except during the winter months from November to March. Starch is absent from all leaves during the winter, but is found at the end of sunny days in March and April. Starch is present in old leaves, except in the winter, right up to the time of death. The supply of carbohydrate was definitely not limiting the rate of respiration in most of the experiments and, therefore, probably did not seriously affect respiration rate even in the winter.

The form of the respiration drift during continuous darkness, and the general relationship of the magnitudes of the three successive 15 min. determinations which are made in all cases on any one occasion, show that there has been no disturbance of rate of respiration as a result of handling the leaves during enclosure in the leaf chamber. There is also no reason to assume any stimulatory effect of exposure to light in these leaves. The rate of respiration appears to remain steady and practically unchanged through the transition from daylight to darkness.

The time of day at which the respiration determinations were made had no effect on the respiration of the leaves (measured at 24.5°C .) except during the winter months, when there was a slight tendency towards low readings before noon. This may possibly be related to the lower level of carbohydrate supply in the leaves at this season, but the effect is hardly appreciable.

Occasion (day of the week) had little effect on respiration of leaves measured at 24.5°C ., although there was a tendency for low respiration readings to follow a period of dull weather at all seasons of the year. Most abnormalities in respiratory activity, however, could not be attributed to variations in weather, either contemporary or previous, or to any other function of the occasion.

The respiratory activity (expressed as c.c. of CO_2 /hr./dm.² of leaf area, at 24.5°C .) was determined at intervals throughout the life of individual leaves. The area of a strawberry leaf does not change appreciably after expansion has been completed (approximately 15 days after emergence of the leaf), and consequently the behaviour of the respiratory activity of any leaf throughout its life is identical with the total respiration of the leaf. Respiration of the leaf increases rapidly during expansion to a peak value which is achieved at about the same time as expansion is completed; there is then a rapid fall to a lower level, which is maintained with only slight further decrease, until the incidence of yellowing, when there is another marked, but temporary, rise in respiration.

All the leaves on all plants behave in almost exactly the same way, except those leaves which are produced in May and June which are much larger than the other leaves. These 'summer' leaves have a high rate of respiration throughout life, and the initial peak is not marked as it is in other leaves. There are definite indications that differences between leaves on the same plant are considerably less than differences between leaves on different, but comparable, plants at the same season of the year.

A comparison of respiratory activity of contemporary leaves on plants of different ages reveals no appreciable difference attributable to age of the plant. No plants older than two years have yet been used, however.

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CONTRIBUTIONS TO THE ECOLOGY OF BRACKEN (*PTERIDIUM AQUILINUM*)

IV. THE STRUCTURE OF THE COMMUNITY

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(With 7 figures in the text)

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The recognition of frond types and their sequence of change across the marginal belt puts us in a position to interpret the structure of the hinterland community on a dynamic basis. Five phases are recognized, four of which include fronds; these four, arranged in the order pioneer, building, mature, degenerate, show the frond types characteristic of the sequence of types across the marginal belt. Since this spatial sequence represents a sequence in time it was concluded that the four phases also form a time sequence. In this contribution further evidence is given to substantiate the conclusion.

The data used also provide a description of the phases. To complete the account of the structure information is also given of the spatial relations between the phases and the relative areas they occupy.

The description applies primarily to area E,* but frequent reference is made to area D,*

* See Part I, *New Phytol.* 39, 401.

especially when area D presents features more sharply defined, and to Red Lodge which was investigated when, during the war, work could not be carried out on areas D and E.

The marginal belt and the hinterland will first be compared as wholes and then particularly.

COMPARISON BETWEEN THE MARGINAL BELT AND THE HINTERLAND AS WHOLE

The number of fronds per unit area of 10 sq.ft. The data in Table 1 show that for the 8 years (1934-41) in area E an average of 22.7 fronds per 10 sq.ft. was found in the marginal belt compared with 18.1 in the near hinterland and 17.8 in the remote hinterland. The differences between these means are not statistically significant. The data show, however, that in most years (1934, 1937-41) the numbers in the margin exceed those in the remote hinterland: in 1935 and 1936 the reverse is true. The numbers in the near hinterland are sometimes closer to those in the margin and sometimes to those in the remote hinterland.

Table 1. *Mean number of live fronds per 10 sq.ft. in the marginal belts of area D and area E and in their respective hinterlands*

Position of sample in relation to front margin	Area D		Area E		
	Marginal belt 0-110 ft.	Near hinterland	Marginal belt 0-80 ft.	Near hinterland 81-110 ft.	Remote hinterland c. 300 ft.
Area of sample in sq.ft. ...	110	103	80	30	192
Year					
1934	—	9.1	19.1	18.0	14.4
1935	31.8	9.2	16.8	18.3	30.8
1936	32.7	—	19.9	26.7	29.1
1937	39.7	—	26.6	19.0	19.5
1938	35.8	—	20.5	24.0	15.3
1939	39.7	—	22.4	18.7	15.5
1940	45.4	—	23.2	6.3	6.0
1941	37.3	—	32.9	14.0	11.5
Mean	37.5	9.15	22.7	18.1	17.8

In area D data for the hinterland over a period of years are lacking, but the available figures show a striking contrast to the number in the margin (37.5 for the margin and 9.15 in the near hinterland). Farther back in the hinterland the number appears to be greater, but there are no exact data.

Comparison between the numbers in the marginal belts of areas D and E shows a much higher number in the better soil of area D; the difference is significant. Also if we set aside the year 1941, when both areas suffered some damage from tanks, the data show a close parallelism in the fluctuations in number over the period 1935-40. On the other hand, there is no such parallelism between the numbers in the hinterland of E and those in the margin except for the years 1937-9. This suggests that factors, presumably climatic, operate upon the marginal populations of areas D and E to produce similar changes in the number of fronds, but that their effect on the population of the hinterland of E is different. This point will be examined more fully in a later communication.

The dispersion of the fronds. In area E the coefficients of dispersion (V/m) of the fronds in the 0-80 ft. of the permanent transect and in sample areas in the hinterland, each of 10×10 ft. in 1936, 1938 and 1939 and 20×20 ft. in 1945, show (Table 2) that in the marginal belt in 6 out of 8 years the fronds are distributed at random, while in the two years 1940 and 1941 they are over-dispersed. In the hinterland, on the other hand, they are over-dispersed in 3 out of 4 years.

Table 2. *The coefficients of dispersion (V/m) of live fronds in August and all emergent fronds (including those killed, mainly by frost) in the marginal belts of areas D and E and in their respective hinterlands. The values in heavy type indicate over-dispersion*

Year	Area D			Area E		
	Marginal belt		Near hinterland	Marginal belt		Remote hinterland
	All fronds	Live fronds in August	Live fronds in August	All fronds	Live fronds in August	Live fronds in August
1934	—	—	3.177	—	1.089	—
1935	1.468	1.305	2.162	1.220	1.040	—
1936	2.169	1.584	—	1.402	1.072	1.52
1937	1.219	1.100	—	0.9425	0.9300	—
1938	0.9555	1.008	—	1.390	1.188	1.403
1939	1.992	1.169	—	1.533	1.045	1.032
1940	1.811	1.904	—	1.654	1.528	—
1941	—	1.672	—	—	1.976	—
1945	—	—	—	—	—	1.491

In the marginal belt of area D over-dispersion is found in 4 out of 7 years, while for the 2 years in the hinterland there is marked over-dispersion.

Comparison between the margins of the two areas shows that in the 7 years for which data are available from both areas, the fronds are randomly distributed in 1937, 1938 and 1939 in both, over-dispersed in 1940 and 1941, and in 1935 and 1936 they are dispersed at random in area E and over-dispersed in area D.

The fronds in the hinterland of area D are obviously patchy (cf. Fig. 1, Part I) and appear to be so in all years in the field in area E. It looks therefore as if the 10×10 ft. sample was not sufficiently large or representative or the data may reflect the fact that the fronds are patchy in some years and not in others.

In this connexion it may be pointed out that the calculations are based on the live fronds in August. In some years, however, many of the emergent fronds are killed by frost. If all the fronds which emerged are used in the calculation then the coefficient of dispersion for 1939 in the hinterland of area E is 1.342, i.e. there is over-dispersion. The live fronds in August, however, include not only the residuum from the total appearing earlier, but also some which would not have emerged had there been no frost. These substitute or replacing fronds, according to the generally accepted view, arise from the same shoots carrying those killed by frost. On this assumption the inclusion of replacing fronds emerging near those killed by frost might account for the over-dispersion. The view, however, is erroneous, at least for area E and Red Lodge for the replacing fronds do not in general arise from the same shoots as those bearing the frosted fronds but from others whose differentiated fronds would not have emerged or whose buds would have lain dormant (*vide* also p. 109). We may, however, eliminate

the replacing fronds by basing the calculation of the coefficient of dispersion on all fronds emerging up to a given date, before which replacing fronds are not expected to appear. Taking this date as 30 June, we find the coefficient of dispersion as 1.414, i.e. there is over-dispersion. The effect of the frost therefore has been to change an over-dispersed population into one distributed at random. While this is so the belief is held that a larger sample would have shown an over-dispersed population, although the value of its measure of dispersion may have been reduced by the differential action of frost.

Such reductions in the values for the coefficient of dispersion are seen in the data from the marginal belts; in area D, four out of the six values for 'all fronds' are higher than those for 'live fronds in August', and in area E all six values are higher. The differences vary; in 1936, 1938 and 1939 in area E they are greater than in 1935, 1937 and 1940. The differentiating factor is the severity of spring frosts: in the former group spring frosts killed many fronds and damaged many of the survivors, in the latter the damage was relatively slight (1935) or negligible (1937, 1940). Much the same applies to the marginal belt of area D, but 1938 and 1940 are exceptions. By and large, therefore, the effect of severe spring frosts is to reduce the values of the coefficient of dispersion.

The dispersion of the depth (age) classes of fronds. The depth classes of fronds have been grouped into four categories and the coefficient of dispersion of each calculated. The results are given in Table 3.

Table 3. *The coefficient of dispersion of depth classes of fronds from the marginal belts of areas D and E and their respective hinterlands. The values in heavy type indicate over-dispersion*

Depth class in in.	Area D		Area E			
	Marginal belt 1935	Near hinterland 1935	Marginal belt 1934	Remote hinterland		
				1936	1938	1939
0-2½	1.811	3.528	1.229	1.742	1.609	1.135
3-4	1.336	1.802	1.012	1.509	1.145	1.028
4½-5½	1.335	1.129	1.301	1.037	0.8797	1.066
5½+	1.585	1.410	1.165	1.037	0.8990	1.313

In the marginal belt of area E (data from 1934 only) all depth classes are at random. In the hinterland there is variation between the categories and within the categories in different years. In 1936 and 1938 the shallowest fronds are over-dispersed, but they are randomly distributed in 1939. In the 3-4 in. depth class the fronds are over-dispersed only in 1936 and in the most deeply set category only in 1939. The 4½-5½ in. depth class shows a random distribution in all three years.

If, however, we base our calculations on all fronds (i.e. including those killed by frost) we get the following values for the categories beginning with the shallowest: 1.785, 1.316, 0.8793, 1.009 for 1938 and 1.648, 2.784, 1.145, 1.485 for 1939. The two shallowest depth categories are over-dispersed, the 4½-5½ in. category at random in both years and the deepest category at random in 1938 and over-dispersed in 1939.

The values for the coefficient of dispersion from the hinterland of area D show the same distribution between the categories. On the other hand, in the marginal belt of area D all the categories show over-dispersion. We may thus conclude that in the hinter-

lands of areas D and E there is a strong tendency to over-dispersion in the shallower (or older) fronds, and a less marked tendency in the deepest set (or youngest) fronds, while the intermediate category ($4\frac{1}{4}$ – $5\frac{1}{2}$ in.) has its fronds distributed at random.

This comparison between the marginal belt and the hinterland brings out certain general resemblances in the number of fronds, in the dispersion of fronds and their depth (age) classes: and also noteworthy differences from year to year apparently caused by the differential action of frost.

PARTICULATE COMPARISON BETWEEN THE MARGINAL BELT AND THE HINTERLAND

The frond

The dimensions of the frond. The hypothesis of cyclic change based on a study of the dimensions of the frond in the hinterland of area E is supported by data from four phases in the hinterland of area D (Table 4; cf. Table 8, Part III). In general the sequence of change in length of parts of the frond and in the ratio lamina/petiole is the same as that found in area E. The fact that the values for the mean depth of origin are the same for the pioneer and building phases is readily accounted for by the presence in the pioneer phase of shallow set relics from the previous degenerate phase as indicated by the figures for the range of depth and for the coefficient of variation. It may further be noted that the range of depth of origin narrows from the pioneer to the mature phase and widens again in the degenerate (cf. Fig. 4, Part III, where the same phenomenon is seen).

Table 4. *Area D. Mean lengths of parts of the frond, the range and the coefficients of variation of depth of origin and number of fronds per unit area in four phases in the hinterland*

Phase	Pioneer	Building	Mature	Degenerate
Size of plot (ft.)			10 × 10	5 × 5	4 × 4	4 × 4
Height of frond in in.			15.25	22.23	26.37	19.85
Length of lamina in in.			14.50	20.80	22.23	17.85
Length of petiole in in.			0.75	1.43	4.14	2.00
Lamina/petiole*			15.66	16.61	6.49	10.92
Depth of origin in in.			5.99	5.99	3.81	4.94
Range of depth in in.			2–13.5	3.5–12.5	2–8	2–11
Coefficient of variation of depth of origin			5.151	4.12	3.647	3.832
No. of fronds per 10 sq.ft.			4.5	24.0	70.0	46.3

* In each phase some of the fronds are of the extreme pioneer type with petioles not reaching or just reaching the soil surface. These fronds were excluded in the calculation of the mean lamina/petiole; the percentages excluded in the pioneer, building, mature and degenerate phases are respectively, 24.0, 16.9, 1.1 and 10.9.

The sequence in the number of fronds across the marginal belt and in four phases of the hinterland. The mean number of fronds in sections of the permanent transects across the marginal belts of areas E and D (Table 5) shows a rapid rise from the front margin to a maximum. This maximum is first reached at approximately the same distance from the outpost fronds in the two areas. In area E, beyond the section where the maximum is first reached, the number fluctuates but is more or less maintained to 70 ft., after which in the last section of the marginal belt (with its limit at 80 ft.) the number drops to a figure approximately the same as in the sections of the transect in the near hinterland

(81-110 ft.). In area D, beyond the first onset of the maximum, there are also fluctuations, but the high number is generally maintained. Just behind the full width of the marginal belt (Fig. 1, Part I) the number drops abruptly, as we have already seen, to the low value of 9.15 per 10 sq.ft. This contrasts sharply with the more gradual change in number of fronds from the margin to the hinterland in area E. There is a similar rise and fall at Red Lodge and at Codson Hill.

Table 5. *Mean number of fronds for the years 1936-41 in sections of the permanent transects across the marginal belts of areas E and D*

Sections in ft. ...	-20 to -11	-10 to -1	1- 10	11- 20	21- 30	31- 40	41- 50	51- 60	61- 70	71- 80	81- 90	91- 100	101- 110
Area E	—	7.3	19.0	23.7	21.3	33.8	29.7	27.2	31.7	19.5	14.2	17.3	22.8
Area D	2	14.2	28.0	34.5	45.3	42.7	33.5	43.0	43.8	48.0	41.5	45.5	46.7

In the pioneer, building, mature and degenerate phases of the two hinterlands the following numbers calculated per 10 sq.ft. are found: in area E (1940) 25, 50, 74, 40 and in area D (1936) 4.5, 24, 70, 46.3. That is, in both the sequence is the same and similar to the rise and fall found in the marginal belt together with the near hinterland. The size of the numbers, especially in the mature phases, is much greater than that in any section of the margin but the fronds are much smaller, and the data in the hinterlands are from selected areas, in area D from a single plot for each phase and for each phase in area E from a number of samples, each of 1 sq.ft., selected on the basis of a number of characters of which number of fronds is one. And the high figures reflect perhaps an undue prominence given to number. At the same time the highest numbers of live fronds found in any single square foot are from the marginal belts of D and E—13 in each area—while in the hinterlands the highest number is 11, found in the mature phase in each of the two areas.

The number of fronds per unit area and the depth of origin. The graphs (Fig. 4, Part III), showing the percentage distribution of the depth classes, brought out clearly the essential identity of the changes taking place with time across the marginal belt and in the four phases. In both there is a shallowing of the mean depth of origin as far as 41-50 ft. in the marginal belt and up to the mature phase in the cycle of change in the hinterland. In the anterior part of the marginal plant there is also an increase in number of fronds per unit area. Comparison may then be made between the depth of origin and the number of fronds per square each of 1 sq.ft. in the 100 squares of 10 × 10 ft. samples taken in 1936, 1938 and 1939 from the hinterland of area E. The mean depths of origin in squares with 1, 2, 3, etc., fronds per square are set out in Table 6, both for all fronds in 1938 and 1939 and for live fronds in those two years and in 1936.

The data for live fronds only and for all fronds show a general drift with the deeper set fronds in squares with few fronds and the shallower set where the numbers are high.

The means of depth of origin for squares with 1, 2, etc., fronds per square obscure the great variation in the means per square, particularly in squares with few fronds. This range is shown in Fig. 1, where the mean depths in squares with a given number of fronds are plotted for the sample area for 1936. With one frond per square the mean depth per square covers the total range of depth found in the plot; the range becomes progressively narrower with an increase in the number per square to quite a narrow

range in squares with 5 fronds. Beyond this the number of squares with 6-9 fronds per square is relatively small; if we take these together we find a tendency towards a wider range in mean depth. There is obviously no correlation between the number of fronds

Table 6. *The relation between the number of fronds per 1 foot square and the mean depth of origin of fronds in area E*

No. of fronds in square ...	1	2	3	4	5	6	7	8	9	10	11	12
Live fronds only:												
1936	3.93	4.35	3.63	3.51	2.63	3.54	3.04	3.81	3.21	—	—	—
1938	4.15	3.29	3.07	3.36	3.05	—	—	—	—	—	—	—
1939	3.40	3.14	3.03	2.92	2.83	3.00	—	—	—	—	—	—
All fronds (i.e. including those killed by frost):												
1938	4.54	3.91	3.91	3.94	3.60	3.49	3.71	3.14	—	—	—	—
1939	3.84	3.43	3.17	3.07	3.45	3.30	2.80	2.44	3.08	3.28	—	2.27

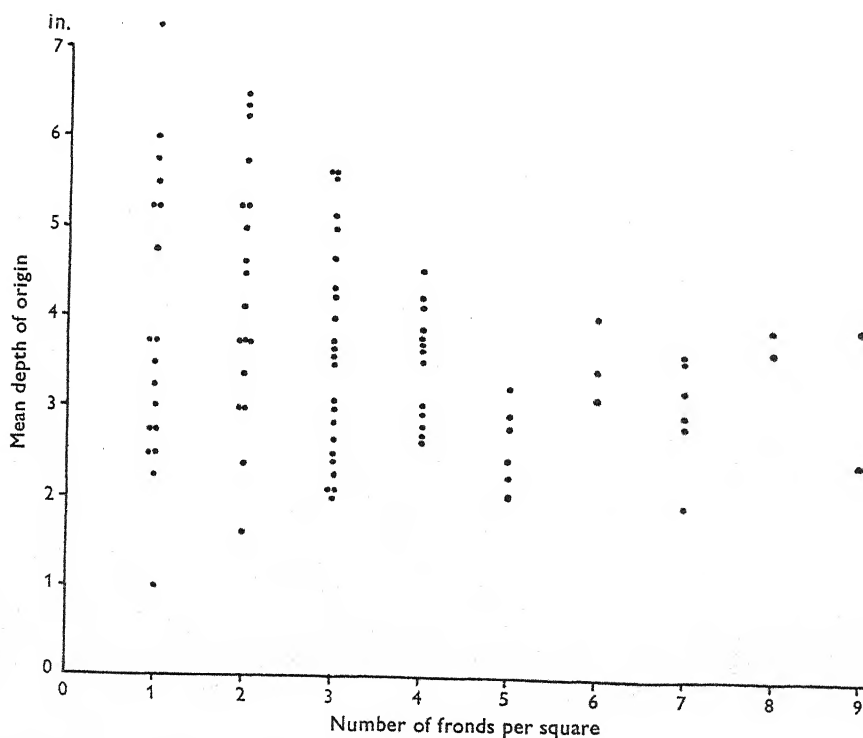


Fig. 1. Area E, hinterland, 1936. The distribution of mean depth of origin of fronds per square of 1 sq.ft. plotted against number of fronds per square. The data are from a 10 × 10 ft. plot divided into 100 squares each of 1 sq.ft.

per square and the mean depth of origin per square; for a negative linear correlation there are too many low means for squares with few fronds and too many high means in squares with many.

But further light is thrown on the relation if we now consider the distribution of depths of the individual fronds in squares with 1, 2, etc., fronds per square (Table 7). The distribution of the depths has been calculated as a percentage of the total found in squares with a given number of fronds and presented graphically in Fig. 2. Where the course of the curves is essentially identical for squares with consecutive numbers the data have been combined. The curves show the same general form and drift in the modes as already brought out in Fig. 4, Part III. Squares with 1 and 2 fronds per square show distribution curves with a wide range of depth and a clear indication of bimodality; squares with 3 fronds show a wide range in depth, a marked skew distribution and a shallow mode. For squares with 4, 5, 6 and 7 fronds the range is much narrower, the curve is less skew and the mode is still shallow. On the other hand, in squares with 8 and 9 fronds the range of depth widens and there is just a hint of a bimodal curve.

Table 7. *Distribution of numbers of fronds in depth categories in 100 squares, each of 1 sq.ft. with 1, 2, 3, etc., fronds per square, 1936*

Depth class in in. ...	0-0.9	1-1.9	2-2.9	3-3.9	4-4.9	5-5.9	6-6.9	7-7.9	8-8.9	Total no. of fronds
No. fronds per square										
1	0	1	5	5	1	4	1	1	0	18
2	0	1	10	5	5	8	3	3	1	36
3	0	8	20	15	11	7	4	1	3	69
4	0	3	17	14	9	4	4	0	0	51
5	0	6	14	8	1	1	0	0	0	30
6	0	0	4	7	6	1	0	0	0	18
7	0	4	16	14	6	1	1	0	0	42
8	0	1	3	5	4	1	1	0	1	16
9	0	4	6	3	3	0	2	0	0	18

Thus in the hinterland the course of change in the percentage distribution of the age classes with increase in the number of fronds per square is similar to that already found in the four selected phases of the hinterland and for selected populations across the marginal belt. The similarity suggests that we are dealing with the same processes. Departures from identity are readily explicable in terms of the hypothesis of cyclic change. The failure to show a correlation between number of fronds per square and the mean depth of origin is due to the fact that in squares with few fronds and to a much less extent in squares with many, we are dealing with mixed populations; in squares with few fronds we find deep-set invading pioneer fronds and shallow-set relict fronds and in squares with many we have an essentially old shallow-set population with some invading deeper-set fronds. That is in squares with many fronds the change in the make-up of the population has already begun just as it begins in the population in the hind portion of the marginal belt.

The diagram (Fig. 3) indicates the changes in the time sequence of the four phases, the overlapping curving lines representing the ideas of change in depth of origin of the frond and, for reasons given in the next section, in age of rhizome and the distribution of young and old rhizome.

The special import of this analysis lies in the objective approach to the study of cyclic change for the data hitherto submitted in support of the hypothesis were obtained from selected samples.

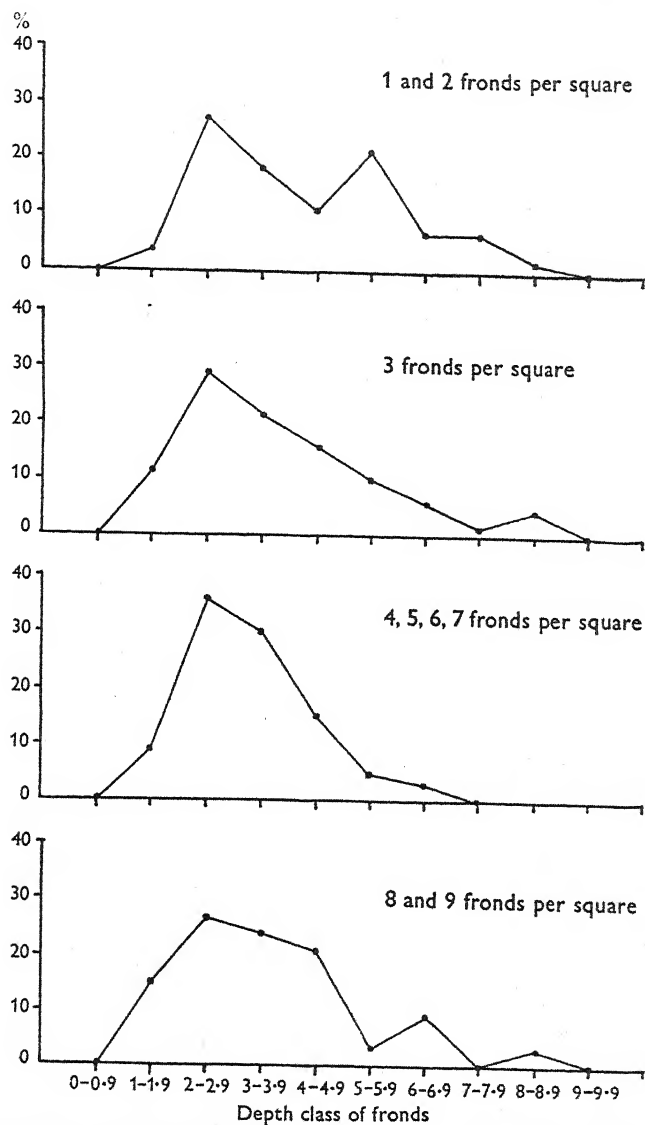


Fig. 2. Area E, hinterland, 1936. The percentage distribution of depth classes of fronds in 100 squares, each of 1 sq.ft., with 1-9 fronds per square.

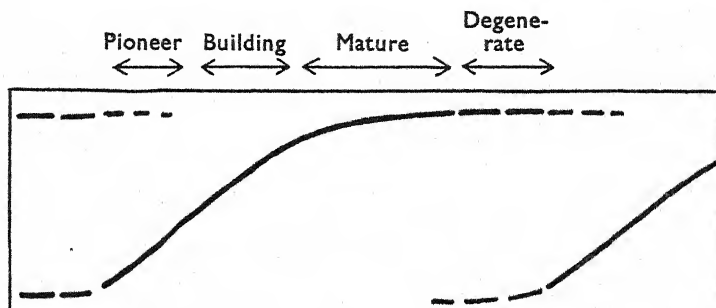


Fig. 3. Diagrammatic representation of the general course of change in depth of origin of the frond, in age of short shoots and the distribution of new and old rhizome. The broken line at the base indicates progressive invasion by new rhizome and at the top death and disintegration of old rhizome.

*The rhizome**Comparison between the length and behaviour of the rhizome in the marginal belt and in the four phases*

The data from the hinterland of area E cannot unfortunately be compared with data from the marginal belt of the same area for none has been obtained. But those from Red Lodge may be used to show the change in length and behaviour of the rhizome across the marginal belt and in the hinterland; these data will then be compared with the data from the hinterland of area E. At Red Lodge pits 2 x 2 ft. were dug in the front margin (at 4 ft. from the outpost fronds), in the region of maximum height of the frond (at 22 ft.), just in front of the end of the marginal plant (at 33 ft.), in the near hinterland (at 45 ft. two pits) and in the remote hinterland (at 75 ft. three pits). In each pit the length of the different kinds of shoot (long, intermediate, short) was measured. Some pieces cut too short for identification are segregated under 'unclassified'. When not too decayed the dead rhizome was also measured.

Table 8. *Red Lodge. Total length in inches of live and dead rhizome per 1 sq.ft. of surface soil and of the different kinds of shoots at selected places across the marginal belt and in the hinterland. The percentage of each kind of shoot is also given*

Distance in feet from front margin ...	Marginal belt						Hinterland			
	4		22		33		Near		Remote	
							45		75	
Live rhizome:		%		%		%		%		%
Length of long shoots	18.1	59.2	116.6	39.9	121.3	41.7	109.3	47.9	112.2	40.6
Length of intermediate shoots	3.0	9.8	54.1	18.5	61.1	21.0	40.3	17.6	53.6	19.4
Length of short shoots	9.1	29.8	115.0	39.4	100.0	34.4	70.0	30.7	100.0	36.2
Length of unclassified shoots	0.4	1.2	6.4	2.2	8.5	2.9	8.6	3.8	10.3	3.8
Total length of live rhizome	30.6	100.0	292.1	100.0	290.9	100.0	228.2	100.0	276.1	100.0
Dead rhizome:										
Length of long shoots	0.0	—	0.0	—	17.1	29.2	38.7	32.1	32.3	30.7
Length of intermediate shoots	0.0	—	0.0	—	3.3	5.5	31.4	26.1	10.3	9.9
Length of short shoots	0.0	—	0.0	—	38.4	65.3	47.2	39.2	49.7	47.3
Length of unclassified shoots	0.0	—	0.0	—	0.0	0.0	3.2	2.6	12.8	12.1
Total length of dead rhizome	0.0	—	0.0	—	58.8	100.0	120.5	100.0	105.1	100.0

Total length of rhizome. The total length of live rhizome (Table 8) rises steeply from the front margin to a high figure at 22 ft.; this high figure is maintained at 33 ft., drops at 45 ft. but is restored at 75 ft. There is no dead rhizome at 4 ft. and at 22 ft., but there is some at 33 ft. and about twice this length at 45 and 75 ft.

Lengths of long, intermediate and short shoots. In the different categories of live rhizome there is also a steep rise in length from the front margin to the region of maximum height; the lengths at 33 ft. are similar to those at 22 ft. with slight rises only in the long and intermediate shoots and a slight fall in the short shoots. At 45 ft. there is a fall in all categories, least in the long shoots, much greater in both the intermediate and short shoots. In the remote hinterland there is little change in the long shoots but in the intermediate and short shoots there is an approximate return to the values found at 33 ft. The data thus show a marked change at 45 ft. that is just behind the marginal plant where reorganization of the marginal community is taking place, the process of change beginning near the end of the marginal belt.

The beginnings of this change at 33 ft. affect the different shoot categories to different degrees. The rise in length of short shoot over the anterior part of the plant is checked and converted to a slight fall and the data for dead rhizome show that 65.3% is made up of short shoots, with 29.2% of long shoot and only 5.5% of intermediate shoot. There is then a proportionately greater dying back of short shoots which is not compensated by the rate of production of new short shoots. The other two categories are much less affected, but the long shoots are more so than the intermediate as might be expected from the morphological relations between them.

At 45 ft. the reorganization behind the marginal belt appreciably involves the long and intermediate shoots as well as the short shoots, for not only is there a fall in all the categories of live rhizome, with proportionately greater falls in the intermediate and short shoots, and an increase in the total length of dead rhizome, but the categories of dead rhizome show a greater proportionate increase in long and intermediate shoots than in the short. We might in fact have expected a greater fall in the length of live long shoot but the loss by death has been offset by a considerable growth of new long shoot (as is seen from the low number of nodes per short shoot (Table 10)). Clearly in the categories of intermediate and short shoot, the loss by death much exceeds the gain. There is in fact at 45 ft. a move in the direction of the distribution of the categories of live rhizome found in the front margin.

At 75 ft. representing the hinterland as a whole the distribution of the categories is much the same as in the hind part of the marginal plant.

In Fig. 4 the percentage contributions made by the different categories are graphed. The curves show the changes more clearly as well as the inverse relation between the long and intermediate shoots, and as might be expected the parallelism between the curves for intermediate and short shoots.

With these data from Red Lodge we may now compare the length of the rhizome and its categories from the four phases of the hinterland of area E (Table 9). The data are the means of a number of samples each of 1 sq.ft. from the four phases. The lengths of the dead long and intermediate shoots were not measured, but the decaying remains were abundant in the mature and degenerate phases, less abundant in the pioneer and least in the building phase. The data from the two areas are not strictly comparable, since the length of the short shoots in area E includes the dead terminal portions where these occur. But since most of the length of dead short shoots at 33 ft. and probably some at 45 ft. at Red Lodge is composed of such dead terminal portions a stricter comparison can be made by adding the length of dead and live shoots together.

Between the contrasted areas certain differences are observed and call for comment. The total length in the front margin is much less than in the pioneer phase, a difference readily understood as due to the relict rhizome present in the latter. Also it was concluded from the evidence of the frond (Part III, p. 170) that the samples of the building phase correspond with a zone in the marginal belt lying between the front margin and the region of maximum height; the shorter rhizome in the building phase as compared with that from the region of maximum height falls into line with this conclusion. Further, if to the data for the live rhizome at 33 and 45 ft. at Red Lodge we add the length of dead short shoots, the values for the total length become 329.3 and 275.4 in., values which approximate those in the mature and degenerate phases.

The lengths of the different categories of the rhizome increase from the pioneer to

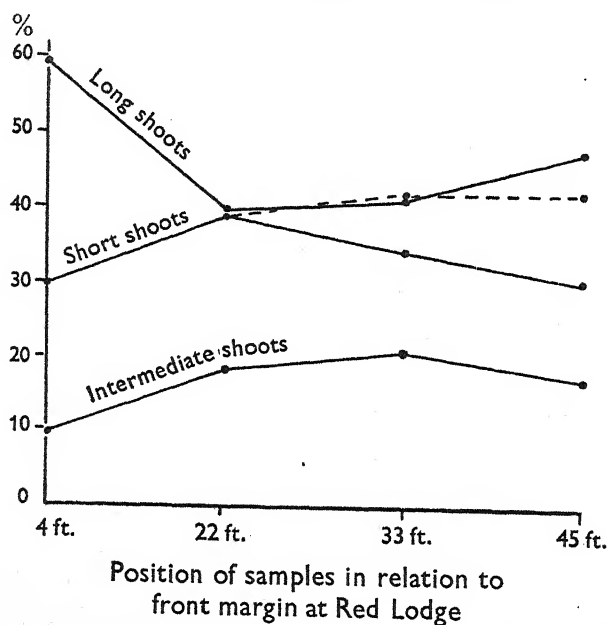
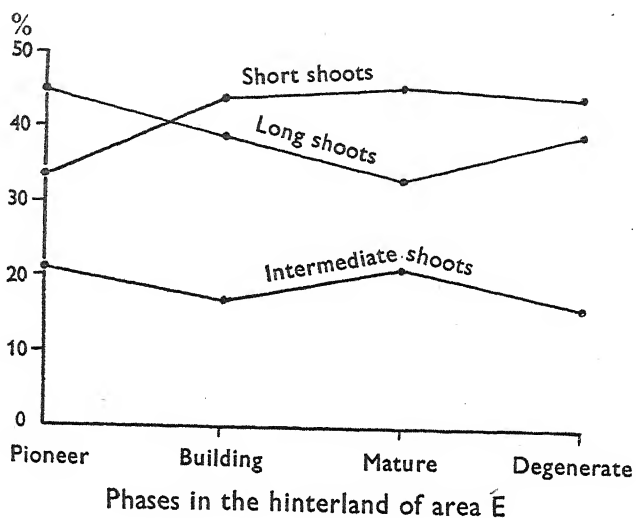


Fig. 4. Comparison between the phases in the hinterland of area E and across the marginal belt at Red Lodge. The plotted points for a given phase show the percentage contributions made by different categories of rhizome in that phase. The graphs show the change in this percentage contribution from phase to phase. The broken line in the graph for Red Lodge is based on the lengths of short shoots including dead ends.

Table 9. *Hinterland E. The total length in inches of rhizome per 1 sq.ft. of surface soil and of the different kinds of shoot in four phases. The data for the short shoots include the length of dead terminal portions where these occur*

Phase	Pioneer	Building	Mature	Degenerate
				%	%	%	%
Length of long shoots				71.4	88.4	115.9	113.1
Length of intermediate shoots				33.8	38.7	75.8	47.0
Length of short shoots				53.8	100.4	160.9	128.2
Total length of rhizome				159.0	227.5	352.6	288.3
				100.0	100.0	100.0	100.0

a maximum in the mature phase. The different courses of the rise can readily be accounted for by reference to the comments in the previous paragraph, namely, to the position of the samples of the building phase in relation to the pioneer and the relict origin of some of the rhizome in the pioneer phase. From the mature to the degenerate phase there is scarcely a fall in the length of the long shoots, but an appreciable one in both the intermediate and short shoots. In this we have a fairly exact parallel with the data from 33 and 45 ft. at Red Lodge, a parallelism emphasized by the changes in the percentage distribution of the categories.

In both the marginal belt and in the hinterland, invasion by the rhizome is directed by ecological opportunity; in the margin into an area free from bracken, in the hinterland into an area vacated by bracken, but still including some relict rhizome. When due allowance is made for this difference the data for total length of rhizome and its several categories show a remarkable correspondence.

The depth of the rhizome. The data for the depth of the rhizome and also for the number of nodes on the short shoots (dealt with in the next section) were obtained from frond-carrying shoots only, in 1940 for the hinterland of area E and in 1942 at Red Lodge (Table 10). (It should be emphasized that the number of frond-carrying shoots may be only a fraction of the total with differentiated fronds, e.g. in a pit 2 x 2 ft. dug in the hinterland at Red Lodge on 27 May 1943 there were 57 shoots with differentiated fronds and only 3 emergent fronds surviving from 1942; similarly on 17 August 1943, there were in a pit of the same size only 8 emergent fronds and 42 more differentiated but non-emergent.) Further, the data from area E are much less complete, especially from the mature phase. Work was begun in this phase, and only when well advanced were data on the depth of the rhizome added to those recorded for the frond and number of nodes on the short shoot. The area was subsequently overrun by tanks, and it may be some years before its normal state is restored.

For the long and intermediate shoots taken together the mean depth varies little either at Red Lodge or in area E, with the exception of the mature phase where the number measured is small. In both areas the mean depth of the long shoots is greater than that of the intermediate in each sample. Further, the sequence of change in depth follows the same course, a fall to a minimum at 33 ft. at Red Lodge and in the mature phase in area E, followed by a rise.

The shallowing of the mean depths of the intermediate and long shoots suggests either that new rhizomes come in at progressively higher levels from the pioneer to the mature phase and the corresponding phases of the marginal belt, the process being reversed in the degenerate phase and at 45 ft.; or that fronds are produced only from rhizomes which lie progressively nearer the surface in the first three phases, and which lie deeper in the reorganizing degenerate phase and in the near hinterland. The suggestion may be tested by comparing the depth of the rhizome and the number of nodes on the short shoot it carries. But some reference is first made to the number of nodes.

The number of nodes. For the long and intermediate shoots taken together there is both at Red Lodge and in area E a rise followed by a fall in the mean number of nodes (Table 10). The difference in the course of the rise is similar to that found for depth of origin and length of rhizome and supports the interpretation already given. There is, however, a difference in the corresponding means, those for area E all being higher, a difference attributable to the survival of old rhizome in the cycle of change, to the

greater mean age of the hinterland population as a whole, and to the greater age attained by individual shoots in the hinterland.

In the contrasted samples of both areas the number of nodes on short shoots arising from long shoots is in general greater than the number from intermediate shoots. The sample at 45 ft. is an exception, which is explained by the reorganization at this place affecting the long shoots to a greater extent than the intermediate. Another exception

Table 10. *Depth of rhizome, number of nodes and the correlation coefficients between them from Red Lodge and the hinterland of area E. Significant correlations are in heavy type. The numbers in brackets are the numbers in the samples on which the data are based*

	Red Lodge			
	Marginal			Near hinterland
Distance from front margin (Red Lodge)	4 ft.	22 ft.	33 ft.	45 ft.
Mean depth of rhizome in in.:				
Long and intermediate shoots	9.91 (31)	10.26 (50)	9.05 (49)	9.36 (49)
Long shoots	12.00 (11)	11.04 (27)	9.88 (34)	10.04 (27)
Intermediate shoots	8.45 (15)	8.27 (14)	7.17 (15)	7.54 (13)
Mean number of nodes:				
Long and intermediate shoots	3.94 (31)	8.92 (50)	9.98 (50)	8.20 (50)
Long shoots	5.55 (11)	9.63 (27)	10.88 (34)	7.78 (27)
Intermediate shoots	3.00 (15)	7.46 (13)	7.40 (15)	7.69 (13)
Correlation coefficients between number of nodes and depth of rhizome:				
Long and intermediate shoots	+0.6270 (31)	+0.2557 (50)	+0.3367 (49)	+0.0460 (49)
Long shoots	+0.3629 (11)	+0.0695 (27)	+0.3805 (34)	+0.0462 (27)
Intermediate shoots	+0.6576 (15)	+0.5640 (13)	+0.0489 (15)	+0.1149 (13)
	Area E, hinterland			
Phase in area E	Pioneer	Building	Mature	Degenerate
Mean depth of rhizome in in.:				
Long and intermediate shoots	11.32 (18)	10.53 (25)	9.33 (9)	11.33 (34)
Long shoots	14.00 (11)	12.53 (16)	9.33 (6)	12.56 (25)
Intermediate shoots	7.13 (6)	6.97 (9)	6.50 (1)	7.92 (9)
Mean number of nodes:				
Long and intermediate shoots	7.24 (21)	9.79 (39)	15.48 (27)	11.59 (41)
Long shoots	9.82 (11)	10.13 (15)	11.00 (6)	14.14 (29)
Intermediate shoots	3.20 (5)	8.36 (14)	14.36 (11)	5.42 (12)
Correlation coefficients between number of nodes and depth of rhizome:				
Long and intermediate shoots	+0.6078 (16)	+0.5718 (25)	+0.5153 (9)	+0.2311 (34)
Long shoots	+0.2615 (11)	+0.6473 (16)	+0.6616 (6)	+0.0461 (25)
Intermediate shoots	+0.0140 (5)	+0.4399 (9)	—	+0.7765 (9)

is found in the mature phase, where the mean from the intermediate shoots is higher than that from the long shoots. But it will be noted that the mean of 27 (intermediate + long) is 15.48, a figure higher than either figure for long or intermediate. This and the small number of long shoots identified suggests the probability that the number is too low to provide a representative sample and that the mean of the long shoots should exceed 15.48. If the mean exceeds 15.48 then the course of change in the number of nodes from long shoots would show a rise then a fall comparable with the rise and fall at Red Lodge. The sequence of change for the intermediate shoots is similar and in this

it differs from that at Red Lodge where there is a rise from 3.00 to 7.46, this figure remaining uniform in the other samples. Thus in the number of nodes there are many points of similarity between the contrasted areas but there are also some differences. Further data are required to confirm or refute a more exact correspondence.

The relation between the depth of the rhizome and the number of nodes. The correlation coefficients (Table 10) show some agreement but many differences between the marginal belt and the hinterland of area E. At Red Lodge for the long and intermediate shoots taken together there is a positive and significant value at 4 ft. and a positive though weak significant association at 33 ft. but not at 22 ft. (where it might have been expected) nor at 45 ft., where reorganization accounts for the very low value. In area E significant values are found in the pioneer and building phases, but in the mature and degenerate phases there is no significant association.

For the long shoots alone there is a significant but weak value at 33 ft. but in none of the other positions at Red Lodge. In area E there is also only one significant value and that is found in the building phase.

At Red Lodge for the intermediate shoots alone the values are significant at 4 and 22 ft. but not at 33 and 45 ft., while in area E the only significant value (there being insufficient data for the mature phase) is found from the data in the degenerate phase.

There is therefore no clear indication of regular change at Red Lodge except perhaps for the intermediate shoots which appear to come in at progressively shallower levels until reorganization of the community begins. It may be pointed out, however, that so long as the community is filling up with new rhizome one or other of the rhizome categories shows a statistically significant value: where, as at 45 ft., reorganization is actively proceeding neither shows it. In the hinterland of area E, where new rhizome grows side by side with old vestigial rhizome, it is probably too much to expect regularity, since the whole is constantly reorganizing in varying degrees of intensity. The numbers used are, however, too small for drawing definite conclusions, but there is sufficient evidence to justify further inquiry along these lines, using the total population of short shoots and not only those bearing fronds in any one year.

The amount and state of the bracken litter

Following the practice of soil scientists the litter may be classified into two layers, the F1 consisting of the more recent additions of dead fronds and the F2 in which disintegration and decomposition are taking place but have not proceeded so far as to eliminate all traces of recognizable frond parts. The frond, after its death, is broken across by wind leaving part of the petiole upright, the lamina falling over. In stout fronds the break usually occurs fairly high in the petiole, so that in the marginal belt the height above ground of the F1 layer is greatest where the fronds are stoutest and tallest, that is, in the region of maximum height; the height falls fairly steeply towards the front margin but only very slowly towards the rear of the marginal belt. The continuity of the F1 layer also varies, depending on the density of the fronds and the action of the wind in throwing the fronds into an uneven cover of discontinuous waves, the crests with a dense somewhat interwoven canopy and the troughs with an open one of few fronds or sometimes none.

The F2 layer, on the other hand, once formed at about 15 ft. from the apex of the plant is continuous to its end. Its thickness increases to 2-4 in. and is maintained at this

level from about 30 to 55 ft. from the marginal outposts, after which it falls towards the limit of the marginal belt, disappearing entirely when the ground is occupied by grass-heath in the gaps formed behind it.

It is thus clear that in the hindpart of the marginal belt the rate of decay of the remains in the F2 layer is faster than the rate of gain. Also in some of the troughs where the F1 layer provides little or no fresh material, the surface of the F2 layer is exposed for a sufficiently long time to become smooth and matted and to change its colour from a light brown to blackish grey.

The sequence of change in the four phases is similar to that described from the marginal belt. In the pioneer phase the few fronds break, the lamina becomes overgrown by grass and decays quickly. In the building phase the F1 layer is more abundant but not continuous and as yet there is no F2 layer, an observation in harmony with the identification of the samples of this phase with a zone just behind the front margin of the marginal belt. On the other hand, in the mature phase there is a continuous F1 layer and a continuous F2 layer about 1 in. thick. Finally, in a typical degenerate phase there is a scanty F1 layer and the surface of the F2 layer has become smooth and discoloured. It also becomes thinner and eventually disappears in the grass-heath phase.

Table 11. *Average abundance of species of grass-heath in the five phases*

Phase ...	Grass-heath	Pioneer	Building	Mature	Degenerate
Species					
<i>Agrostis</i> spp.	3.9	3.0	2.6	0.0	1.3
<i>Festuca ovina</i>	2.0	1.0	1.5	0.0	1.0
<i>Luzula campestris</i>	2.0	2.5	1.5	1.0	2.0
<i>Rumex acetosella</i>	2.0	2.0	2.3	1.0	2.0
<i>Aira praecox</i>	—	1.0	—	—	—
<i>Galium saxatile</i>	2.0	—	—	—	1.0
<i>Calluna</i> seedling	One	—	—	—	—
<i>Dicranum scoparium</i>	3.0	2.7	2.0	1.0	2.0
<i>Hypnum cupressiforme</i>	3.7	1.5	1.0	1.0	1.7
<i>Polytrichum juniperinum</i>	3.0	1.5	—	—	—
<i>Hypnum schreberi</i>	—	—	—	—	2.0
<i>Ptilidium ciliare</i>	2.1	2.1	1.5	—	2.0
<i>Cladonia silvatica</i>	3.4	3.6	3.5	—	1.3
<i>C. pyxidata</i>	2.0	1.0	—	—	—
<i>C. furcata</i>	1.0	1.0	—	—	—
<i>C. bacillaris</i>	1.0	—	—	—	—
<i>C. coccifera</i>	1.0	—	—	—	—
<i>C. uncialis</i>	—	2.0	—	—	—
<i>Cetraria aculeata</i>	2.0	1.0	—	—	—
Total no. of spp. ...	16	14	8	4	10

The accompanying species

No records have been made of the details of the change in the floristic composition of the grass-heath following invasion by bracken, but the species of the grass-heath are ultimately completely eliminated by the canopy of live fronds and the F1 and F2 layers. And only after the bracken opens out behind the marginal belt do the species of the grass-heath come in again.

This finds a parallel in the sequence of the four phases. In the list of species (Table 11) abundance is expressed on a semi-statistical basis by equating dominant with 5, abundant

with 4, etc., and averaging the data for a number of plots for each phase. The results are indicative only as the number of samples is small.

From the data provided it will be seen that the total number of species falls from the pioneer to the mature and then rises in the degenerate. The species progressively eliminated by the bracken are primarily the more pronounced heliophilous and small *Aira praecox*, *Polytrichum juniperinum*, *Cetraria aculeata*, and the *Cladonias* other than *C. silvatica*. The other species in general show from the pioneer to the mature phase a fall in abundance or are eliminated altogether from the mature phase, where four species only are found and each is rare.

The plant remains below the bracken litter

The replacement of the grass-heath phase by bracken in the hinterland of area E is further confirmed by the presence of recognizable remains of *Festuca ovina*, *Agrostis* sp., *Rumex acetosella*, and *Dicranum scoparium* below the F2 layer in the mature and degenerate phases. This, of course, is paralleled in the marginal belt by the complete suppression of the grass-heath by bracken and the presence of identifiable remains of some of its components, particularly *Festuca ovina* and *Agrostis* sp. under the F2 layer.

The spatial relations of the phases

Examples of the several phases are repeated again and again throughout the hinterland community. Together they form its mosaic or pattern, and a single set of representative phases we may call the unit of the pattern or simply the unit pattern. The data given for the frond, the rhizome, the accompanying species and the litter of the hinterland of area E form a partial description of the community based on samples of the same area from four phases. To complete the account of the structure, however, it is necessary to refer to the texture of the pattern, that is, to the way in which the phases are distributed and to the relative areas occupied by them. The account also provides further evidence for the dynamic interpretation of the structure and is supported in the next section by observations on the time relations of the phases.

The distribution of the phases in space. As we have seen the sequence in space in the marginal belt represents a sequence in time. In the hinterlands of areas D and E similar sequences, complete or partial, are found; they are particularly clear in area D where the pattern is coarser, less so in the finer textured pattern of area E.

Fig. 5 is based on data obtained from the hinterland of area D, from a transect 1 ft. wide running from the margin of a roughly circular patch of bracken to its centre. From the outside inwards the sequence of change in frond dimensions and number per unit area is similar to that across the marginal belt: the chief difference is that in the patch the zonation is concentric instead of linear.

In time such a patch grows larger and the bracken withdraws from the centre in ever-widening circles (Fig. 1, Part I). Such hollow circles (or interrupted arcs of them) are seen up to 50 ft. or more in diameter, and may show inside them all phases from degenerate to mature. The retreating margin is the degenerate phase. Next to it is the grass-heath phase of variable width; within it are scattered fronds which increase in number towards the centre of the circle. These fronds are of two types, small relict fronds from weak short shoots of small plants of relict rhizome and deep-set pioneer fronds arising from the descending intermediate and long shoots which are extensions of the short

shoots of some of these relict plants. Towards the centre one or more circular patches of denser bracken may be found with short fronds on the margin and tall fronds in the centre. Thus a complete sequence may be found along a line from the retreating margin to the centre of the recolonizing patch.

The circles are seldom complete; more often they are in the form of crescents and discontinuous arcs. Where two neighbouring colonies spread and impinge, patches are formed in which the smallest fronds are in the middle and the tallest on the outside near the retreating margins. Such patches become smaller with time and eventually disappear.

The whole structure of the bracken community in the hinterland of area D can be interpreted in terms of dynamically related phases. The phenomena described are widespread not only in Breckland but throughout the country, and are particularly obvious in some parts of Wales where the bracken is not too tall and dense.

In area E the spatial relations are not so diagrammatic. The examples of the phases occupy smaller areas, and the smaller differences in the height of the bracken in juxtaposed phases (particularly in years of crippling frost as were 1936, 1938 and 1939) make

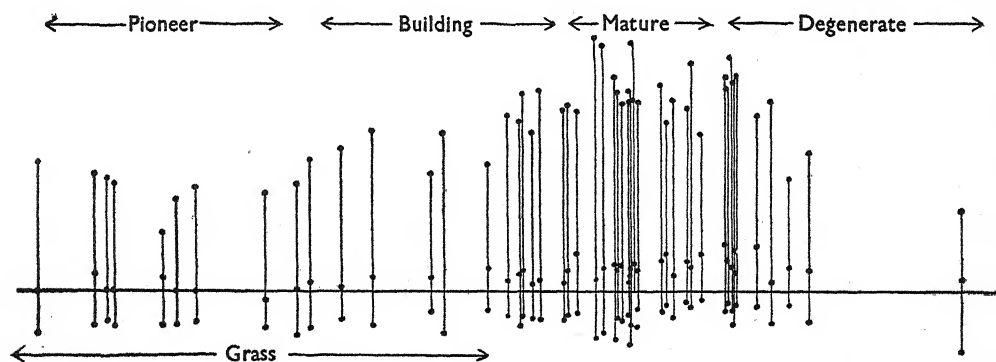


Fig. 5. The positions and dimensions of the fronds in a transect 13 ft. long and 1 ft. wide along a radius of a circular patch of bracken showing the sequence of phases from pioneer to degenerate. The dots indicate the depth of origin, petiole length and height of fronds. The vertical and horizontal dimensions are on the same scale.

the sequences less sharply defined. But in Fig. 6, the chart showing the distribution of the fronds and the phases for 1938, the phases are clearly not haphazard, and partial sequences are readily distinguishable.

The relative areas occupied by the phases in area E. Across the marginal belt the change is continuous, and limits imposed on the zones corresponding with the phases of the hinterland are somewhat arbitrary. The grass-heath in front of the marginal belt corresponds with the grass-heath phase of the hinterland; its outward limit is indeterminate. The first 10 ft. of the transect we may equate with the pioneer phase, the next 15 ft. (from 11 ft. to the middle of the region of maximum height at 25 ft.) with the building phase. These limits are fairly clear cut. Beyond the region of maximum height readjustment in the make-up of the population begins, increases towards the limit of the marginal belt and is completed in the near hinterland. Hence on the hinterland side the zone corresponding to the degenerate phase is indeterminate and in the marginal belt itself may be somewhat arbitrarily put at 15 ft. from its posterior limit. This leaves a width of 40 ft. representing the mature phase.

In the hinterland the areas occupied by the several phases have been computed from the 10×10 ft. plots for 1936, 1938 and 1939 (Fig. 6). The selection of typical phases is easy, but the assignment to its phase of each square foot of the area is often difficult because of the intergradation of the phases, the damage caused by frost and because the limits of the phases rarely coincide with the limits of the squares. Thus the decisions respecting some squares are somewhat arbitrary although the number of doubtful cases is surprisingly small. The data are given below:

Year	Grass-heath phase	Pioneer phase	Building phase	Mature phase	Degenerate phase
1936	9	16	33	30	12
1938	11	12	15	29	33
1939	3	7	8	59	23
Mean in round numbers	8	12	19	39	23

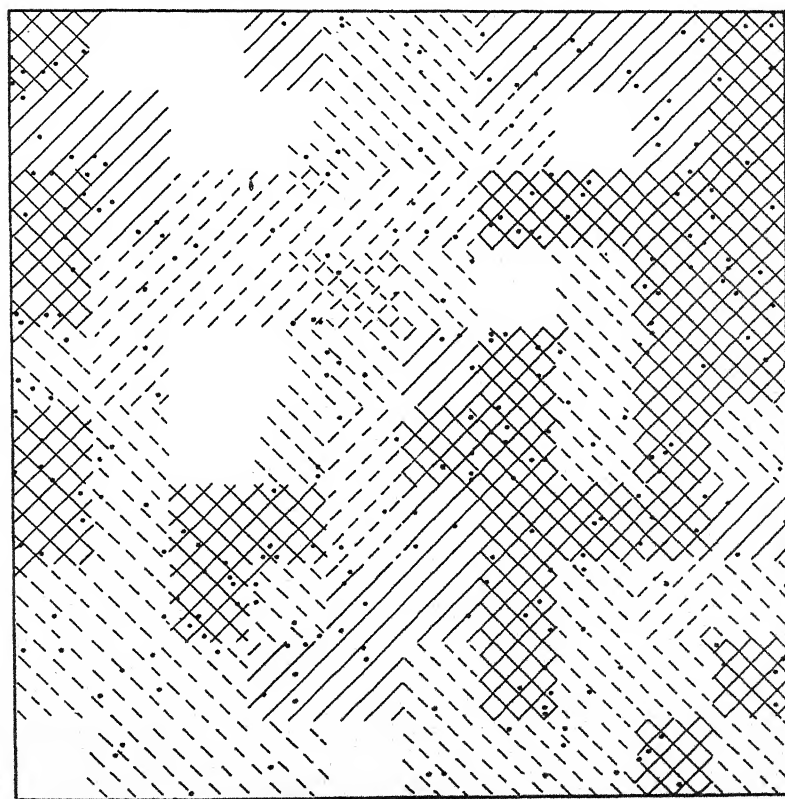


Fig. 6. Chart of the 10×10 ft. plot examined in 1938 showing the distribution of the fronds (black dots) and the spatial relations of the phases. Blank squares = grass-heath; // pioneer; // building; ×× mature; ×× degenerate.

The means for the pioneer, building and mature phases show close agreement with the figures for the corresponding zones in the marginal belt; the building phase occupies an area half as large again as the pioneer and less than half that of the mature. If this is the normal state then we may conceive of a phasic equilibrium when the relative areas occupied are in the proportions of the means.

But there is much variation between the years. Two possible reasons may be suggested. The first, and more likely in this area, is that the sample is too small to be fully representative and the figures suggest that a sample of 300 sq.ft. would be nearer the mark. The alternative possibility is that the variation is due to the incidence of some exceptional factor like burning, cutting or the removal of the litter, all of which in an area liable to frost would tend to upset the phasic equilibrium and increase the earlier phases at the expense of the later. Depending on the degree of the interference the effects of the throw-back may last many years. From 1931 to 1940, however, none of these exceptional factors operated in the hinterlands of area E or D. Bracken litter is fairly regularly removed in winter from Lakenheath Warren, and the taller and denser bracken of area D would present a more attractive area for exploitation than area E. If area D has been so exploited prior to 1931, then we have a possible explanation of the texture of the pattern found in the hinterland, for the grass-heath, pioneer and building phases occupy much larger areas than their representation in the marginal belt would lead us to expect.

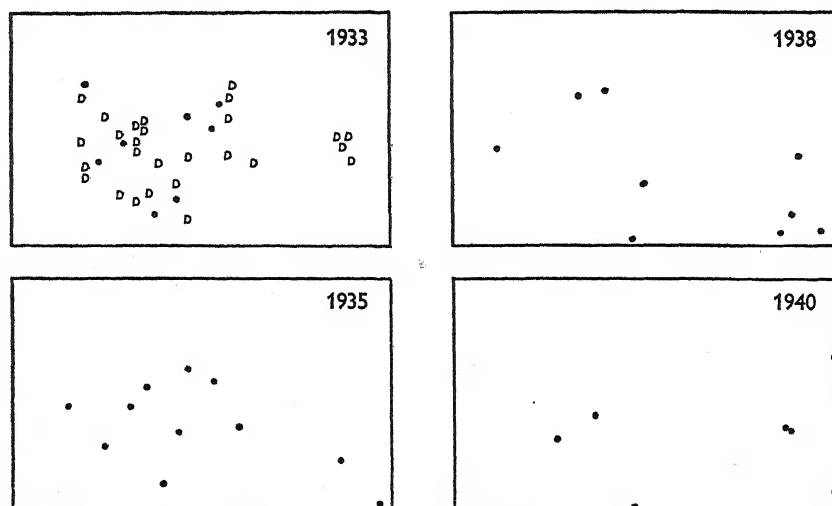


Fig. 7. Charts showing the positions of live fronds in a plot 5 × 3 ft. for the years 1933, 1935, 1938 and 1940. The letter *D* in the chart for 1933 marks the positions of fronds produced in the years immediately preceding 1933.

The time relations of the phases

The change in time at a given place. The formulation of the concept of cyclic change was initiated in part by the observation that patches of fronds of previous years were repeatedly found, in some places surrounded by live fronds, in others detached with no live fronds within several feet. The vacation of the ground by bracken, proved by the existence of the decaying fronds, was put to the test, and Fig. 7 is a record of the change in the position of the live fronds over the period 1933–40 in a locality near to areas D and E. The plot of 5 × 3 ft. shows two patches of fronds surrounded by the grass-heath phase. The letter *D* in the chart for 1933 indicates the positions of the fronds of previous years. The record shows the migration of the fronds in subsequent years away from the original concentrations. Part of the grass-heath phase is passing into the pioneer and the original mature phase into the degenerate.

Proof that the bracken is retreating on the inner side of the marginal belt in area D (and the phenomena suggesting retreat are exactly the same in comparable positions in the hinterland) is obtained from plots laid down in 1932. The records from one of the plots, 36 in. wide by 18 in. deep, located in the retreating margin show the following numbers of live fronds from 1932 to 1945, omitting 1941-4 inclusive: 10, 23, 17, 20, 25, 23, 14, 5, 7 and 0. The fluctuations in number in the earlier years generally reflect the variation in the frond population over the area as a whole; in the later years the decline is due to the withdrawal of the bracken. In 1945 the plot was completely covered by grass-heath, and the nearest frond on the retreating margin to the inner boundary of the plot was 11 in. distant.

The course of change in the cycle is not necessarily smooth. We may, at this stage, assume that certain factors accelerate the rate of change, whilst others retard it or cause retrogression. The most important causing retrogression is frost. A plot in the hinterland of area D, judged in 1936 to be in the building phase, was, through the serious crippling spring frosts of 1938 and 1939 and the even more damaging winter frosts of early 1940 and 1941, thrown back to the pioneer and virtually to the grass-heath phase. For the years 1936-41 and 1945 the numbers of fronds in the plot of 4 x 3 ft. were 29, 21, 16, 36, 2, 5 and 6, and the change in number was accompanied by a phasic change in frond dimensions; the petiole lengths for example were 1.71, 3.35, 3.71, 1.73, 1.00, 1.90 and 3.75 in. Over the same period (except for 1945, when no record was made) a somewhat similar change in number and petiole length was recorded in the -10 ft. to -1 ft. section of the transect in area D; the numbers were 12, 22, 17, 16, 5 and 13 and the petiole lengths 1.63, 2.71, 5.76, 1.61, 1.50 and 2.53 in.

This fluctuation is also reflected in the year to year position of the outpost fronds of the bracken invading the grass-heath. Over the period 1936-41 there was a general advance, the outposts in 1941 being 3 ft. ahead of those in 1936, but in 1940 they were 3 ft. behind, a recession due to the severe winter frost of early 1940. Thus in areas liable to frost the measurement of the rate of advance of bracken based on one or two years' records is of little value.

The duration of the cycle and of its phases. Theoretically it should be possible to compute the duration of the cycle and of its phases. With the material available there are two lines of approach for an estimate, the first based on the rate of advance of the bracken, the second on the number of nodes as an estimate of age.

For the reason just given it is difficult to get an estimate of the mean rate of advance which would be applicable to the whole period of time taken by the bracken to traverse the width of the marginal belt. An estimate of the rate of advance into grass-heath type E, based on the period 1932-40 inclusive, gives a mean rate of approximately 1 ft. per annum. On this assumption the marginal belt has taken 80 years to traverse its own width, and the duration of the pioneer, building and mature phases would respectively be 10, 15 and 40 years; the minimum duration of the degenerate phase would be 15 years.

There are no data of the number of nodes from the marginal belt of area E, but we may utilize those from Red Lodge to see how far the estimate of duration based on number of nodes agrees with the estimate based on rate of advance. Assuming at Red Lodge a rate of advance of 1 ft. per annum, then the 36 ft. wide marginal belt represents a minimum duration of 36 years and the phases corresponding with the pioneer, building,

mature plus part of the degenerate occupy respectively 10, 12 (22-10) and 14 (36-22) years. The maximum number of nodes found in these phases respectively is 8 (excluding the figure 13 for reasons given in Part II), 19 and 32 giving values for duration of 8, 11 and 13. There is thus a high degree of correspondence between the two methods of assessment. It is possible and, indeed, likely that the value of 13 for the mature phase plus part of the degenerate based on the number of nodes is too low, for in this part of the belt the old short shoots die back and the chances of obtaining in a pit 2 x 2 ft. a complete live short shoot which has persisted from a marginal outpost are small. We may, however, accept the figures as indicating the relative periods of time occupied by the phases. Their translation into absolute values rests on the assumption of a rate of advance for which there is no evidence and on the number of nodes which, as we have seen in Part I, is an unreliable guide to age.

Because of the dispersion of the phases in the hinterland of area E the same technique of assessment based on rate of spread cannot be readily applied. Nor, because of the overlapping of phases in the cycle of change, can an estimate be obtained from the number of nodes. Moreover, the conditions are different, the plants are smaller and they grow at a slower rate. But the duration of the phases may be comparable with that in the marginal belt.

The problem may be approached in another way. In the marginal belt of area E the unit of length is convertible into the unit of time, and without altering the absolute values the unit of space may be substituted for the unit of length. Hence it is possible to equate the space occupied by the phases in the transect with duration in years. In the ideal community we may assume that the space occupied by the phases stands in direct proportion to their duration. On this basis of computation the data for the areas occupied by the phases will also give their relative duration. Now for the marginal belt the duration of the pioneer, building and mature phases is 10, 15 and 40 (total 65) years; for the hinterland 12, 19 and 39 (total 70) years. In an approximation of this kind these values are sufficiently near to be treated as equivalent. On this basis, therefore, the complete cycle of change in the hinterland of area E lasts about 100 years and the grass-heath, pioneer, building, mature and degenerate phases in round numbers respectively, 8, 12, 19, 39 and 23 years. It should be emphasized that these values are computed from an estimate of rate of advance during a period within which occurred an exceptionally long drought and an exceptionally severe winter frost: it may well be that over the last 80 years the rate of advance was significantly greater.

CONCLUSION

The interpretation of the structure of the stable community of bracken as a series of dynamically related phases is facilitated by the existence at its margin of a transient belt showing a specialized arrangement of the component individuals. The marginal plants have their axes radiating outwards with their apices approximately in line. The plants are large, and their form is affected by freedom to spread outwards into the grass-heath and by checks to lateral spread through competition with neighbouring plants. The result of this juxtaposed alinement is the formation of a belt in which parts of the plants of the same morphological age lie side by side in zones parallel with the front of advance.

From the advancing front across the marginal belt there is a regular sequence of change in the dimensions of the frond, related to the position of the frond on the plant, to the general ecological conditions of the area and to these as affected by the plant itself. There is also a change in the number of fronds and in the length of the rhizome and its categories. There is, in fact, a gradual filling up of the soil to saturation point near the region of maximum height.

From the front margin to the region of maximum height, the change in all these is uniformly progressive. Beyond this region readjustment begins and increases towards the end of the plant; the fronds become smaller with age of the short shoot, the old short shoots die back and are replaced by younger carrying more vigorous fronds, and towards the limit of the marginal belt the main rhizome itself dies. Thus the graded series of relatively even-aged populations of the anterior part gives way to a population becoming increasingly uneven-aged in the posterior, although the percentage of old fronds remains high.

This sequence of change in space is proved to represent a sequence in time by the morphology of the plant itself, by the amount and state of the bracken litter and by the presence of remains of species of the grass-heath below the litter. Observations over a period of years also prove the advance in position of the marginal outpost fronds.

On the death of the main axis, the lateral branches become independent plants to form in the hinterland a community on a new and stable plan. The axes of the plants (which are much smaller than in the marginal belt) form a network, and the general form of the individual is irregular because it is unequally affected by the uneven distribution of competition and of the opportunity to spread. Over a period of years the mean number of fronds is much the same as in the marginal belt, but the fronds are much smaller and fail to cover the ground completely, leaving patches to which the components of the grass-heath return. From place to place the fronds vary in number and dimensions; so also do the amount and state of the litter and the species of grass-heath. All these are linked in such a regular way that it is possible to pick out patches (phases) representative of the continuous change. In addition to the grass-heath phase, four phases with fronds have been selected and called, respectively, the pioneer, building, mature and degenerate phases.

The comparison of the four phases with fronds, with selected populations across the marginal belt, shows such close agreement in the sequence of change in frond dimensions, in number of fronds, in the length of the rhizome and its categories and in the make-up of the populations that the conclusion is reached that these four phases represent a sequence in time. And further proof of their identity is afforded by the similar sequence in the kind and amount of the litter and in the presence of the remains of species of the grass-heath below the litter in the mature and degenerate phases. The full cycle of change includes the grass-heath phase, for in it is found much dead and often some live rhizome. Occasionally in the hinterland the five phases are seen forming a sequence in space similar to that across the marginal belt; more commonly partial sequences, resulting from the impact and fusion of adjoining centres of spread, are found. The differences between the cycle of change in the hinterland and in the marginal belt are attributable to the different conditions and mainly to the invasion in the former of areas vacated or partly vacated by bracken, whereas in the margin invasion of bracken-free ground takes place.

The immediate cause of the similarity between the marginal belt and the hinterland is the biological consequence of invasion. Once invasion takes place the rest follows as a matter of course; there is a gradual filling up of the invaded area by long, intermediate and short shoots and the fronds they carry. But the course of the change is not necessarily smooth. Within the general developmental change there are fluctuations; in some years there is retrogression, in others an acceleration of the rate. Moreover, the factors affecting it may have different effects on the different phases.

Each of the five phases is repeated again and again over the hinterland, and the relative areas occupied by each is different. Together they form the mosaic or pattern of the community. A single set of phases representative of the processes and their manifestations in the cycle of change we may call the unit of the pattern or simply the unit pattern. This unit is the essence of the whole. An understanding of the mutual relations and behaviour of the constituent phases of the unit provides the key to an understanding of the whole community in a way not brought out by existing methods of investigation.

The phases are not distributed in a haphazard way; juxtaposed phases often bear sequential relations to each other. Also the phases are represented by patches of different sizes, and the total areas occupied by each phase in the community vary. The area occupied by each sample of a phase, the total relative areas occupied by them and the way the phases are distributed, together determine the texture of the pattern. When the texture is in equilibrium with the normal environment we may expect a normal areal distribution of the phases in a state of equilibrium with each other. This phasic equilibrium may be upset by exceptional environmental factors whose effects may last long after the factor has ceased to operate.

The application of this approach to the study of other plant communities and its implications in studies on the nature of the plant community will be dealt with elsewhere. In the meantime let it suffice to say that the interpretation of the community on a dynamic basis serves to link the phenomena of the community with those of the relations between communities in a sere and to emphasize the underlying uniformity of the nature of vegetational processes.

SUMMARY

There are two main objectives: to provide supporting evidence for the hypothesis of cyclic change formulated in Part III, and to present the basis of a new method of describing plant communities in terms of the dynamically related phases of the cycle of change.

The transient marginal belt and the stable hinterland are first compared as wholes. The number of fronds per unit area and their coefficients of dispersion vary from year to year and between the contrasted wholes and are probably more affected by frost than by any other single factor. In the hinterland there is a clear tendency for the older age classes to be over-dispersed.

In the particulate comparison of the marginal belt with the hinterland it is shown that the five phases recognized in the hinterland (grass-heath, pioneer, building, mature, degenerate) have their counterparts in the zones (phases) of the sequence across the marginal belt together with the flanking grass-heath and the near hinterland. The equation of the two sets of phases is based on evidence from the frond (its dimensions,

number per unit area, and the contribution made by different frond types to the make-up of the population) and from the rhizome (its total length per unit area, the length of its categories of long, intermediate and short shoots, the depth of the long and intermediate shoots and the number of nodes on the short shoot); also from the amount and state of the litter, the accompanying species and the distribution of the phases in space.

The phases of the marginal belt represent a sequence in time. From their correspondence with the phases in the marginal belt and from internal evidence it is shown that the phases in the hinterland also represent a sequence in time. This conclusion is supported by observational evidence over a period of years on the change in time at a given place. An attempt is made to compute the duration of the whole cycle and of its phases.

The mosaic or pattern of the community is formed of the phases, and a single representative set of them is called the unit pattern. Across the marginal belt they form an obvious zoned spatial sequence; in the hinterland they are dispersed through the community but not in a haphazard way. A chart shows their spatial relations.

This unit pattern is the essence of the whole community, is the basis of its description and has the advantage over existing methods in combining an account of processes with their manifestations. To complete the description, data are given on the relative areas occupied by the phases; these, together with data on the area occupied by individual samples of the phases and the way in which they are distributed, constitute the texture of the pattern.

It is suggested that when a community is in equilibrium with its normal environment there will be a normal areal distribution of the phases forming a phasic equilibrium. The incidence of exceptional factors will upset this equilibrium, and its effects may last long after the factor has ceased to operate.

I should like at this stage in the record of results to express my gratitude for various kinds of assistance: to Lord Iveagh, through his agent Mr J. A. Dow, for placing labour and the ground at my disposal; to several friends for help in the laborious task of digging up fronds and rhizomes, and in particular to Mr N. P. Mohan and my former assistant Mr R. A. Peachey; to Dr (now Professor) A. R. Clapham for help in the field and to him and to my colleagues in the Botany School for advice on statistics; and to the Royal Society and to the British Association for the Advancement of Science for financial assistance during the earlier stages of this work.

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BUXUS SEMPERVIRENS IN A LATE ROMAN BURIAL IN BERKSHIRE

DATA FOR THE STUDY OF POST-GLACIAL HISTORY OF BRITISH VEGETATION. XI

By J. ALLISON

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(With 1 figure in the text)

This plant material was found by the head and legs of a skeleton, and apparently lined the floor of a lead coffin, which was in one of a series of Late Roman graves dug in chalk on Roden Down, Compton, Berks, excavated by Mr M. S. F. Hood who sent the material to Dr Godwin (Ref. No. R.D./P. 207/22. Grave IX).

The material consisted of loosely compacted layers of small shoots and was recognized as leaves and young stems of *Buxus sempervirens* L., of which, however, nothing but cuticle was preserved. The cuticles of a few whole leaves were recovered with the characteristic ovate shape, recurved margin, freedom from indication of lateral veins, and short,

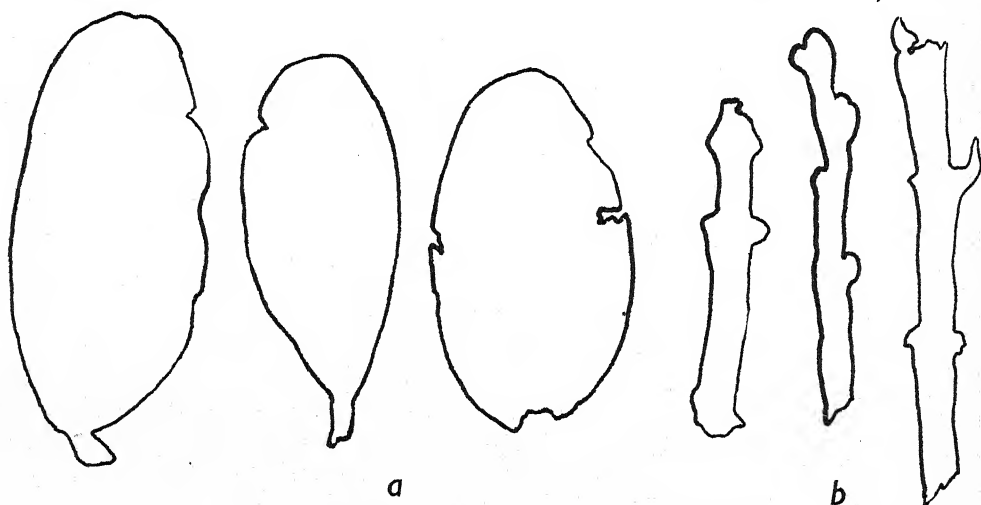


Fig. 1. *Buxus sempervirens*, L. a, leaves; b, stems. $\times 3$.

twisted petiole. In several pieces of stem the decussate leaf arrangement could be seen. The cuticles were compared with those prepared from living material of *Buxus* by heating in 10% NaOH. In both instances a characteristic stomatal pattern was seen on the leaf cuticle, though as the stomata are slightly sunken they had often dropped out. The stems had a characteristic pattern of alternation of hairy ridges and bands of hair-free stomata-bearing cuticle. A fragment of material resembled the fruit of *Buxus*.

The identification has special interest because of the view often expressed that the box is not native in Britain, and because of the restricted natural distribution of the shrub at the present day in England.

NOTES ON THE CLASSIFICATION AND DISTRIBUTION OF GENERA RELATED TO *GOSSYPIMUM*

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INTRODUCTION

This account of genera related to *Gossypium* is in the nature of a supplement to the study of the taxonomy of *Gossypium* published elsewhere (Hutchinson, 1947). It was undertaken primarily to complete the classification of species excluded from *Gossypium* on taxonomic and cytogenetic grounds, and to clear up the confusion that existed concerning the limits of *Gossypium*.

Underlying the treatment of species differentiation here adopted is Vavilov's (1935) theory of the nature and distribution of variability in cultivated plants. He has shown that the great bulk of the variability in such species is concentrated in a comparatively small part of the range, and has postulated that variability is one of their natural characteristics, and the areas in which it is greatest are those in which the species originated. The theory has proved very valuable in tracing the evolutionary history of the cultivated species of *Gossypium*, and a close correspondence between areas of high variability and centres of specific, varietal and racial differentiation has been demonstrated (Hutchinson & Silow, 1947). Recently Mayr (1942), discussing species differentiation in birds, has emphasized the fact that the development of the discontinuity characteristic of a true specific distinction can only take place in geographical isolation.

It is suggested, first that Vavilov's analysis of the distribution of variability applies to wild as well as to cultivated species, and secondly that Vavilov's and Mayr's principles together provide a valuable guide in determining species limits where genetic and cytological evidence is not available. Consider the spread of a single, somewhat variable, species into new habitats. So long as the distribution remains continuous, the whole remains effectively a single interbreeding population, and the establishment of discontinuity will be prevented by gene exchange. Response to different selective forces in different parts of the range may result in the establishment of ecotypes, the extreme forms of which may for convenience be given varietal names. So long, however, as they are

united by clines maintained by gene exchange over a continuous distribution, these ecotypes are genetically unstable and depend for their continued existence on the continuance of the selective forces that brought them into being. If the continuity of the distribution is broken, divergence both under different selective forces and at random (the Sewall Wright (1940) effect) will take place and will be irreversible, and a real discontinuity will arise which will justify recognition as of specific rank. Such a new species may remain small and uniform, adapted to its particular ecological niche, but not spreading. Alternatively, by the development of a new character or by some accident of the environment that opens up a considerable area which it is well fitted to colonize, it may multiply and spread. The genetic consequences of evolutionary success have been discussed by Hutchinson & Stephens (1947*b*), who have concluded that once the process of multiplication and variation has begun, it will tend to be cumulative, so that a successful species will become variable and, having become variable, it will have the capacity to respond to selection that is the condition of further success. Naturally, it will be in the areas of the initial success that the greatest variability will be built up, and the distribution of variability which Vavilov (1935) found in successful crop plants may therefore be regarded as a genetic consequence of evolutionary success that is valid for any species, and is not confined to cultivated organisms.

If this view of the process of species development is accepted, related forms that are wholly 'sympatric', to use Mayr's term, can only be regarded as specifically distinct if the existence of some other isolating mechanism (e.g. polyploidy) is demonstrated. Moreover, where distinct, but related, species are partially sympatric, it should generally be possible to show that their distributions were originally distinct, and only overlapped after successful spread from their original centres. The wild species of *Gossypium* meet these requirements, since they are in general well isolated. In *Cienfugosia* and *Thespesia*, however, many of the forms that have been given specific rank are sympatric. Examination of herbarium material and of published descriptions showed that sympatric species were often difficult to separate, or were regarded by some authors as synonymous. A wider interpretation of the species has been adopted here and it will be shown that the genera can be divided into natural species which now occupy, or give evidence of having originated in, geographically distinct areas. Moreover, the distribution of the variability within these species is as would be expected if Vavilov's principle applies.

THE RELATIONSHIPS OF THE GENERA

Edlin (1935) has proposed that the Malvaceae should be confined to genera with septically dehiscent schizocarpic fruits, genera with loculicidally dehiscent capsular, or baccate, fruits, being included in the Bombacaceae. The whole of the Hibisceae, in which the genera here considered are included, are thereby transferred from the Malvaceae to the Bombacaceae.

For present purposes the Hibisceae may be divided into a large group with reniform seeds and free, capitate style branches, and a small group of seven genera with rounded, compressed, or turbinate seeds, and with the styles usually joined and clavate, and only rarely free or capitate.

These seven genera may be distinguished as follows:

- A. Oil glands on the calyx confined to a double row along each nerve. I. *Cienfugosia*.
- AA. Oil glands on the calyx scattered, sometimes absent—B.
- B. Calyx truncate or 5-undulate, sometimes drawn out into 5 widely separated teeth—C.
- C. Capsules dry and brittle when ripe—D.
- D. Stigmas free. II. *Gossypioides*.
- DD. Stigmas joined, clavate—E.
- E. Bracteoles 3, ovate, triangular, or strap-like. III. *Gossypium*.
- EE. Bracteoles 4-6, in 3 groups, filiform. IVa. *Thespesia lampas*.
- CC. Capsules woody or leathery when ripe—F.
- F. Flowers borne on simple pedicels, or on jointed peduncles with only minute bracts at the joint. IV. *Thespesia*.
- FF. Flowers borne on jointed peduncles, each peduncle bearing a large caducous bract at the joint. V. *Kokia*.
- BB. Calyx 5-lobed or 5-parted—G.
- G. Involucre of 3 small, free, often caducous bracteoles. VI. *Notoxylinon*.
- GG. Involucre shallow 5-7-toothed cup. VII. *Alyogyne*.

The species of *Gossypium* have been discussed in detail elsewhere (Hutchinson, 1947). Those of *Cienfugosia*, *Gossypioides* and *Thespesia* are dealt with below. No adequate material is at present available on which to base full descriptions of the rest.

The genus *Cienfugosia*

Cienfugosia Cav., *Fugosia* Juss., *Redoutea* Vent. Small glabrous or variously hairy perennial *shrubs*, or perennial *herbs*, springing from woody rootstocks. *Leaves* entire, toothed, or variously lobed. *Flowers* solitary and axillary on simple pedicels, or on jointed peduncles, or borne several together on sympodial or racemose inflorescences. *Involucral bracteoles* 3- ∞ , free, linear or filiform, persistent or caducous, often minute, or rarely absent. *Calyx* joined at the base, divided above into five ovate acute lobes: *lobes* 3-nerved; *oil glands* on the calyx confined to a double row along each nerve. *Anthers* ∞ , unilocular, arranged on short filaments arising from a staminal column. *Stigmas* joined, clavate, or ending in a stigmatic disc or capitate, or free with or without capitate tips. *Capsules* loculicidally dehiscent, 3-5 locular, with several seeds per loculus. *Seeds* usually long and narrow, almost naked, hairy or densely woolly.

The type of the genus is *Cienfugosia digitata* Cav.

Eleven species are recognized here. Three (*C. welshii*, *C. hildebrandtii* and *C. gerrardii*) form a geographical and morphological series, distributed from Somaliland and the Aden Protectorate in the north to Natal and the Transvaal in the south. The type of the genus, *C. digitata*, is widely distributed on the western side of the African continent, from Mauretania to Bechuanaland. *C. heteroclada* is limited to grass savannah country in northern Nigeria.

In the New World, the four species *C. heterophylla*, *C. yucatanensis*, *C. cuneata* and *C. argentina* form a geographical and morphological series, with a distribution from Florida, through the Lesser Antilles, the Spanish Main and Yucatan, down western South America to the Argentine. *C. affinis* has its centre of variability in the Guianas and eastern Venezuela and is widely spread in Brazil, and *C. sulfurea* has its centre of variability in Paraguay but only spreads as far as Uruguay and the northern Argentine.

Two species recently described by Chiovenda have been omitted from consideration as they fall outside the limits of the genus as here defined. *C. (Synodontos) chiarugii* from Somaliland is excluded on the gamophyllous involucre and on the distribution of the oil

glands on the calyx. *C. althaeoides* from Kenya has an involucre of five ovate bracteoles that are connate for the lower third of their length. Six species (*C. anomala*, *C. triphylla*, *C. areysiana*, *C. somalensis*, *C. ellenbeckii* and *C. bricchettii*) have been transferred to *Gossypium* (Hutchinson, 1947).

The species of *Cienfugosia* may be distinguished as follows:

- a. Flowers borne on jointed peduncles or sympodial fruiting branches—b.
 - b. Leaves dentate along the upper margin—c.
 - c. Stigmas joined, capitate. 1. *C. welshii*.
 - cc. Stigmas joined, clavate. 2. *C. hildebrandtii*.
 - bb. Leaf margin entire 3. *C. gerrardii*.
- aa. Flowers borne in racemes, or singly on simple pedicels—d.
 - d. Flowers borne in racemes arising from the base of the previous season's stem. 4. *C. heteroclada*.
 - dd. Flowers borne singly on simple pedicels—e.
 - e. Involucral bracteoles less than $\frac{1}{2}$ as long as the calyx, or absent—f.
 - f. Involucral bracteoles 6–12—g.
 - g. Stigmas clavate—h.
 - h. Staminal column only antheriferous above. Leaves $\frac{1}{4}$ cut or digitately divided. 5. *C. digitata*.
 - hh. Staminal column antheriferous throughout—j.
 - j. Herbs springing from a perennial woody rootstock. Leaves entire or shallowly divided. 6. *C. cuneata*.
 - jj. Small, upright, perennial shrubs. Leaves usually entire, rarely shallowly divided or even ternate. 7. *C. heterophylla*.
 - gg. Stigmas capitate. 8. *C. yucatanensis*.
 - ff. Involucral bracteoles absent. 9. *C. argentina*.
 - ee. Involucral bracteoles more than $\frac{1}{2}$ as long as the calyx—k.
 - k. Style ending in a stigmatic disk. 10. *C. affinis*.
 - kk. Style ending in free capitate stigmatic branches 11. *C. sulfurea*.

(1) *C. welshii* (T. Anders.) Garcke. Small *shrub* with a woody rootstock, practically glabrous. *Leaves* cuneate at the base, abundantly toothed along the upper margin, entire, shallowly 3–5-lobed, or deeply divided into 3–5 main lobes, which are also shallowly subdivided. *Flowers* borne singly on jointed peduncles. *Involucral bracteoles* 3, more or less divided, usually into 8 or 9 linear, inconspicuous bractlets arranged in 3 groups. *Calyx* cup divided into 5 ovate acute lobes, interspaces between the lobes narrow acute; *lobes* 3-nerved; *oil glands* on the calyx confined to a conspicuous double line along each nerve. *Stigmas* joined, capitate. Ripe *capsules* about thrice as long as the calyx lobes. *Seeds* copiously hairy.

DISTRIBUTION. Aden Protectorate and Somaliland. Area of high variability Somaliland, where a wide range of leaf form is found. Aden material is uniform in leaf type, all specimens being shallowly lobed.

(2) *C. hildebrandtii*. Garcke. *Chromosome* number $2n=22$. Small perennial woody *shrub*. *Leaves* finely hairy, cuneate at the base, entire, almost triangular in outline, with a number of small teeth along the upper margin. *Flowers* usually borne singly on jointed peduncles that are about the same length as the petioles, occasionally two or three together on short sympodial fruiting branches. *Bracts* at the joints of the peduncles and nodes of the fruiting branches small (3–5 mm. long). *Involucral bracteoles* 6–10, arranged in 3 groups, free, minute. *Calyx* cup divided above into 5 ovate acute lobes, the interspaces between the lobes narrow acute; *lobes* 3-nerved; *oil glands* on the calyx confined

to a conspicuous double row along each nerve. *Stigmas* joined, clavate. Ripe *capsules* about twice as long as the calyx lobes. *Seeds* copiously hairy.

DISTRIBUTION. Coastal Kenya, Tanganyika (Usambara), southern Nyasaland, Southern Rhodesia (Zambesi valley), eastern Transvaal, Swaziland, northern Natal, Portuguese East Africa. The distribution and ecology of the species in the eastern Transvaal and Natal have been extensively surveyed by Marshall, Parsons & Hutchinson (1937). They found that its upper altitude limit was 1200–1500 ft. and that below this level it was confined to areas of good soil in three habitats, '(a) the crests and sloping sides of low elevations, (b) along water channels and (c) pans (vleis)', and they concluded that 'the evidence clearly indicated that the primary focus is one on the crests and slopes of low hills and eminences that have a good soil cover, the other occurrences being consequent on proximity to water courses'.

(3) *C. gerrardii* Harv. *Thespesia rehmannii* Szyszyl. Small perennial woody shrub. *Leaves* glabrous, cordate, broadly ovate or reniform in outline, bluntly 3-lobed or entire. *Flowers* borne singly or in twos or threes on short sympodial fruiting branches. *Leaves* at the nodes of the fruiting branches fully developed, but small. *Involucral bracteoles* 3, free, minute. *Calyx* cup divided above into oblong acute lobes with rounded interspaces between; *lobes* 3-nerved; *oil glands* on the calyx confined to a rather inconspicuous double row along each nerve. *Stigmas* joined, clavate. *Seeds* thinly hairy.

DISTRIBUTION. Ladysmith and East Griqualand in Natal and Lydenburg and Middleberg in the Transvaal, Swaziland. Marshall *et al.* (1937) state that this species is only reported from the easterly margin of the middle veld districts in the Union of South Africa and Swaziland. They found it 'in colonies growing in scanty soil in hilly ground above altitudes of 1400 ft.'

These three species form a geographical sequence, replacing each other from north-east to south-west without overlapping. Morphologically also they form a natural series. They are the only species in the genus with the flowers borne on jointed peduncles or sympodial fruiting branches. All specimens of *C. welshii* examined had jointed peduncles. In *C. hildebrandtii*, jointed peduncles are the common form, but they occasionally develop into fruiting branches of 2 or 3 nodes. The leaves at the nodes of the fruiting branches seldom develop into more than very small bracts. In *C. gerrardii* the inflorescences vary from single-jointed peduncles to 2- or 3-jointed sympodial branches, and the leaves at the nodes are fully developed though small. In leaf shape, there is a gradation from *C. welshii* with cuneate, many-toothed or dissected leaves, and *C. hildebrandtii* with cuneate, many-toothed leaves, to *C. gerrardii* with the leaves cordate, broadly ovate, bluntly 3-lobed or entire. The involucre also shows the evolution of many small bractlets from a basic three.

(4) *C. heteroclada* Sprague. Low undershrub sending up shoots, after burning, from a woody rootstock. *Leaves* large, glabrous, entire or slightly lobulate, tapering to the base, ovate, very shortly acuminate above. *Flowers* borne close to the ground on racemose inflorescences made up of special reduced branches arising from near the base of the previous season's stem. *Pedicels* longer than the short petioles. *Involucral bracteoles* 3, free, small and inconspicuous. *Calyx* cup $\frac{1}{3}$ cut into acute lobes, interspaces between the lobes narrow, angular; *lobes* 3-nerved; *oil glands* on the calyx confined to a double row along each nerve. *Stigmas* free, not capitate. Ripe *capsules* $1\frac{1}{2}$ times as long as the calyx. *Seeds* covered with a dense coat of bristly, rust-coloured hairs.

DISTRIBUTION. Northern Nigeria. *C. heteroclada* is a specialized type adapted to the ecological conditions of dry savannahs that are frequently burnt in the dry season.

(5) *C. digitata* Cav. Stems annual, herbaceous from a perennial woody rootstock. Leaves glabrous, not cordate, digitately divided into usually 3, rarely 5 or 7, linear or oblanceolate lobes, or $\frac{4}{5}$ cut into 3-7 lobes that are further cut into subsidiary lobes at the apex. The lower leaves are usually broader and more subdivided at the apex, and the upper leaves more deeply divided with oblanceolate lobes. Flowers axillary, solitary, pedicels simple, about twice as long as the petioles. Involucral bracteoles 6-12, free, minute. Calyx cup deeply divided into narrow acuminate lobes that are larger than the bud, the interspaces between the lobes narrowly angular; lobes 3-nerved; oil glands on the calyx confined to a conspicuous double row along each nerve. Anther filaments arising from the upper part of the staminal column only. Anthers arranged almost as a ball. Stigmas, joined, clavate. Ripe capsules rounded, rather shorter than the calyx lobes. Seeds densely woolly.

DISTRIBUTION. Mauretania, Senegambia, Senegal, French Sudan, Angola, Ngamiland, Northern Rhodesia, northern Transvaal, Bechuanaland, South-West Africa. The Bechuanaland and South-West African material is highly variable in leaf form. That from Angola, Ngamiland and Northern Rhodesia generally has the leaves $\frac{4}{5}$ cut into 3-7 main lobes that are subdivided, while types from the Sudan and North Africa region usually have digitately divided leaves with linear or oblanceolate lobes.

The area of greatest variability of *C. digitata* is in the southern part of its range, so following Vavilov in taking the area of high variability as the centre of origin, the northern areas of its distribution in the West African savannah countries may be regarded as areas of later colonization, and the overlapping of the area of *C. heteroclada* as secondary. *C. digitata* does not appear to overlap the distributions of any of the East African species.

(6) *C. cuneata* Bth., *C. anemonoides* Spruce. Perennial herb growing from a woody rootstock. Leaf form variable, usually deltoid entire, or nearly so, below, becoming broadly 3-lobed in the middle of the plant, and lanceolate entire, or almost linear above. Flowers solitary, axillary, on long simple pedicels that are much longer than the petioles. Involucral bracteoles, c. 10, free, inconspicuous, less than $\frac{1}{2}$ of the length of the calyx lobes. Calyx cup $\frac{4}{5}$ cut into long acuminate lobes which exceed the bud in length; lobes 3-nerved; oil glands on the calyx confined to a double row along each nerve. Staminal column antheriferous throughout. Anthers arranged in the form of a cylinder. Style only slightly exceeding the staminal column in length. Stigmas united, clavate. Capsules rounded, glabrous. Seeds hairy.

DISTRIBUTION. South Ecuador (Ancon and Chandery) and Peru (Paita and Talera). Grows near the Pacific coast, in full exposure, under a normal rainfall of 6-8 in.

(7) *C. heterophylla* (Vent.) Garcke. *C. punctata* Turcz., *C. tripartita* Steud., *C. cuyabensis* Pilger. Chromosome number $2n=20$. Small perennial glabrous or puberulent shrubs. Leaves entire, narrowly lanceolate, ovate acute, or broadly ovate; rarely shallowly 3-lobed or even ternate. Flowers solitary in the axils of the upper leaves. Pedicels simple, much longer than the petioles. Involucral bracteoles 6-10, free, minute, less than $\frac{1}{2}$ as long as the calyx. Calyx cup about $\frac{2}{3}$ cut into long tapering lobes, longer than the flower bud; lobes 3-nerved; oil glands on the calyx confined to a double row along each nerve. Staminal column antheriferous throughout. Anthers arranged in the form of a cylinder. Style less

than twice as long as the staminal column. *Stigmas* joined, clavate. *Capsule* rounded, glabrous. *Seeds* hairy.

DISTRIBUTION. Florida Cays, St Thomas, Trinidad (Chacachacare Island), Curaçao, Venezuela (Margarita Island, and La Guaira), Colombia (Santa Marta), Brazil (Piauhy, Bahia, Jaen de Bracamoros, and Matto Grosso). There is something of a cline in leaf shape in this species. The narrowly lanceolate entire Florida and West Indian forms give place to the ovate acute and broadly ovate forms of Margarita Island and Santa Marta. These in turn yield to the Brazilian types, in which shallowly 3-lobed leaves are found and even the more or less deeply tripartite or ternate leaves of the form described as *C. tripartita* from Jaen de Bracamoros.

(8) *C. yucatanensis* Millsp. Small perennial shrub. *Leaves* glabrous, linear or linear-lanceolate entire. *Flowers* axillary on long peduncles. *Involucral bracteoles* 5-9, free, minute, awl-shaped. *Calyx* 5-parted into slender lanceolate lobes; lobes 3-nerved; *oil glands* on the calyx confined to a double row along each nerve. *Style* 6 mm. long. *Stigmas* joined, capitate. *Seeds* bearing a dense coat of ferrugineous wool.

DISTRIBUTION. On arid stony soil, 6 km. south of Progreso, Yucatan.

(9) *C. argentina* Garcke. *C. escholtzioides* Hoch., *C. hassleriana* Hoch. Perennial herb springing from a woody rootstock. *Leaves* puberulent or nearly glabrous, sometimes shallowly 3-lobed, sometimes deeply cut into 3 main lobes which bear shallow subsidiary lobes. *Flowers* solitary on simple pedicels that are much longer than the petioles. *Involucral bracteoles* absent. *Calyx* cup $\frac{1}{2}$ cut into long acuminate teeth, longer than the bud; lobes 3-nerved; *oil glands* on the calyx confined to 2 rows along each nerve. *Style* nearly twice as long as the staminal column, divided at the top into capitate stigmas. *Capsules* rounded, glabrous; *seeds* hairy.

DISTRIBUTION. Northern Argentine and Paraguay. Hochreutiner's *C. escholtzioides* and *C. hassleriana* are large forms from Paraguay.

The four species *C. heterophylla*, *C. yucatanensis*, *C. cuneata* and *C. argentina* form a natural group. Variability in leaf form is very pronounced among them, as indeed it is throughout the genus, and it is chiefly on this account that *C. tripartita* and *C. cuyabensis*, which differ from *C. heterophylla* in little more than the shape of the leaves, are here sunk. The species are strictly allopatric, and are separated from one another by formidable geographical barriers. The leaf form of *C. heterophylla* in the western parts of its distribution approaches that of *C. cuneata*, which is found on the Pacific coast of Ecuador. These two species are characteristically plants of dry coastal areas, and the spread of forms of *C. heterophylla* inland into central Brazil where it approaches the northern limits of the distribution of *C. argentina*, may reasonably be regarded as secondary. The affinities of *C. argentina* are more with *C. cuneata*, across the Andean ridge, than with *C. heterophylla* in its southward extension in Brazil. *C. yucatanensis* may be regarded as a northward extension of the group, with *C. heterophylla* in Colombia as its nearest relative.

(10) *C. affinis* (St. H.) Hoch., *C. phlomidifolia* Garcke, *Fugosia campestris* Bth., *F. guianensis* Klotzsch, *F. retusa* Turcz., *C. riedelii* Garcke. A shrubby plant 3-5 ft. high, usually moderately to densely tomentose, sometimes puberulent. *Leaves* elliptical, oblong or oblong-lanceolate, margin entire. *Flowers* borne singly in the axils of the upper leaves, on simple pedicels that are considerably longer than the petioles. *Involucral bracteoles* c. 9, free, linear, about the same length as the calyx lobes. *Calyx* cup about $\frac{1}{2}$ cut into long acuminate lobes that exceed the bud in length; *oil glands* on the calyx obscured by

the dense tomentum. *Style* much longer than the staminal column, ending in a stigmatic disk. *Capsules* ovoid acute usually copiously hairy. *Seeds* bearing only short and scanty hair.

C. phlomidifolia, *Fugosia campestris*, *F. guianensis* and *F. retusa* have been sunk in *C. affinis* by Hochreutiner. *C. riedelii* is here sunk, as it only differs from the type in being more tomentose, and in so variable a species such a difference is of no consequence.

DISTRIBUTION. British Guiana, Venezuela, Colombia, Brazil (Matto Grosso, Minas Geraes, Goyaz, Amazonas, Piauhý) Paraguay.

The centre of variability of the species is in the Guianas and neighbouring areas, whence a number of forms have been described as separate species. Its southern extension, where it overlaps *C. sulfurea* and *C. argentina*, may safely be regarded as secondary.

(11) *C. sulfurea* (St. H.) Garcke. *C. subprostrata* Hoch., *C. drummondii* A. Gray. Small perennial shrub, with a woody rootstock, puberulent or glabrous. *Leaves* subrotund or ovate, irregularly dentate, crenate or entire. *Flowers* borne singly in the axils of the uppermost leaves on long simple pedicels. *Involucral bracteoles* 5-8, free, more than $\frac{1}{2}$ as long as the calyx lobes. *Calyx* cup $\frac{3}{4}$ cut into long acuminate lobes; *lobes* inconspicuously 3-nerved; *oil glands* on the calyx inconspicuous, confined to a double row along each nerve. *Style* greatly exceeding the staminal column in length, divided at the tip into short capitate stigmas.

C. subprostrata Hoch. is the *C. sulfurea* var. *integrifolia* of some authors. It differs from the type in having larger flowers, on very long pedicels, and entire leaves. *C. drummondii* is a large flowered form, but has dentate leaves. There is no reason to believe that these forms are more than chance isolations from a rather variable species. *C. drummondii* has been recorded from Texas. In view of the facts that it is not distinct from the South American *C. sulfurea*, and has only been found in Texas rarely and at long intervals of time, the possibility that it may have been introduced from South America should be investigated.

DISTRIBUTION. Uruguay, northern Argentine and Paraguay.

The centre of variability of the species is in Paraguay and secondary extensions to its area are not great.

Reviewing the genus as a whole, differentiation has occurred along three tracks in Africa and three in South and Central America. In Africa the greatest differentiation has been on the eastern side of the continent, where a morphological cline has been interrupted in two places, giving rise to three allopatric species. On the western side of the continent, successful northward spread from a south-western focus has gone on without the establishment of isolation barriers, and the wide ranging *C. digitata* shows no sign of fragmentation into subspecies. *C. heteroclada* is the result of a specialized evolutionary trend, and is neither widely spread nor variable.

In South and Central America the *heterophylla* group of species has arisen from the isolation of segments of a population occupying the north and west coasts of South America, and stretching over the middle Andean chain into the northern Argentine. The four species are strictly allopatric and the most widely distributed (*C. heterophylla*) is the most variable. *C. affinis* forms an interesting parallel to *C. digitata*, having spread widely from a variable centre (in the Guianas) without encountering isolation barriers of sufficient importance to give rise to discontinuity. *C. sulfurea* appears to be successful in its own area, having given rise to sufficient variability for two of its forms to be given specific

names, but it has not spread widely over the continent in the way *C. affinis* has done. Though *C. affinis*, *C. sulfurea* and *C. argentina* are partially sympatric it will be seen that if this interpretation of their spread is correct, they were strictly allopatric in their origin, and were specifically distinct before their areas of distribution began to overlap.

The genus *Gossypioides*

The genus *Gossypioides* was proposed by Skovsted (1935) for the wild East African shrub described by Masters as *Gossypium kirkii*. Harland (1932) first excluded it from *Gossypium* on the grounds that it will neither graft nor hybridize with any known *Gossypium*, and that it possesses square stems. Skovsted (1935) showed that it differs from *Gossypium* in chromosome number, having a complement of $2n=24$ instead of $2n=26$, and in the stigma lobes, which are free. Unfortunately, he published no description.

The genus includes the two species originally described as *G. kirkii* M. Mast., and *G. brevilanatum* Hoch. *G. brevilanatum* and some types of *G. kirkii* have stems that are ribbed or angled when young, but not square, so Harland's morphological criterion requires modification. The failure of grafts with *Gossypium* has been confirmed for both species. In addition to Harland's (1932) record, the following *Gossypioides* \times *Gossypium* crosses have been attempted:

Gossypium hirsutum \times *Gossypioides brevilanatum*.

Gossypium barbadense \times *Gossypioides brevilanatum*.

Gossypioides brevilanatum \times *Gossypium anomalum*.

Gossypium arboreum (tetraploid form) \times *Gossypioides kirkii*.

Gossypium arboreum (tetraploid form) \times *Gossypioides brevilanatum*.

All were shed in 4 or 5 days, as they would be if left unpollinated. The crossing barrier is therefore complete, pollination failing even to stimulate ovary development.

The morphological differences from *Gossypium*, though few, are important. The free stigma lobes are very distinctive, and the ribbed, angled, or winged stems are also characteristic. While in many genera the difference between 24 and 26 in chromosome number would be of little significance, it must be regarded as important in the delimitation of *Gossypium*, in which aneuploidy is unknown in nature and extremely rare in experimentally produced material. In addition there are certain indefinable features of leaf form and texture which make species of *Gossypioides* look unlike *Gossypium*, and it may be concluded that there are good grounds for accepting Skovsted's separation.

The genus may be described as follows:

Gossypioides Skovsted (ex J. B. Hutchinson *genus novum*). Suffrutex subscandens. Folia 3-7-lobata. Stipulae falcatae, acuminatae. Bracteolae 3, ovatae, inciso-dentatae. Calyx breviter 5-dentatus. Columna staminea filamenta ∞ exserens. Ovarium 3-5-loculare; loculi 2- ∞ ovulati; styli rami 3-5. Capsula loculicide dehiscens. Semina subglobosa.

The type of the genus is *Gossypioides kirkii* (M. Mast.) J. B. Hutchinson, comb. nov. Chromosome number $2n=24$. Subscandent woody shrubs. Stems, petioles and pedicels ribbed, angled or winged. Branches of two kinds, monopodial vegetative branches and sympodial fruiting branches. Leaves 3-7-lobed. Stipules falcate, persistent. Bracteoles 3, free, large, ovate, serrate or gashed, persistent. Calyx truncate, minutely 5-pointed, or 5 undulate. Anthers ∞ , unilocular, compactly arranged on short filaments arising from a staminal column. Stigmas free, not capitate. Capsules loculicidally dehiscent,

3-5-locular, with short hairs on the sutures, 2-10 seeds per loculus. *Seeds* ovate, almost naked or bearing a fine coat of rusty red hairs.

Two species are known, *G. kirkii* from East Africa and *G. brevilanatum* from Madagascar. They may be distinguished as follows:

a. Bracteoles about as long as the petals, deeply cordate.

aa. Bracteoles less than $\frac{1}{2}$ as long as the petals, narrowed to the base.

1. *G. kirkii*.

2. *G. brevilanatum*.

(1) *G. kirkii* (M. Mast.) J. B. Hutchinson comb.nov. (Syn. *Gossypium kirkii* M. Mast. (1882)). *Chromosome* number $2n=24$. Perennial, much branched, sprawling *shrub*, up to 2 m. tall. *Stems* ribbed, angled or winged. *Leaves*, *petioles*, *pedicels* and young *stems* finely hairy or almost glabrous. *Fruiting branches* sympodial, many jointed. *Leaves* large, deeply cordate, $\frac{2}{3}$ -palmatifid into usually 5, rarely 7 lobes. *Nectaries* on the main veins above the level of the leaf sinuses. *Stipules* large and very conspicuous, broad, oblique, clasping the stem, persistent. *Bracteoles* large, persistent, deeply cordate, divided along the upper margin into 10-15 acute or acuminate teeth. *Petals* hardly exceeding the bracteoles in length, deep golden yellow. *Staminal column* rather short, antheriferous throughout. *Filaments* short, all about the same length. *Stamens* rather compactly arranged, often in five ranks. *Stigmas* free, spreading. *Capsules* 3-4 locular, almost spherical; each *loculus* containing two basal ovules, the whole of the rest of the cavity being filled with a mass of short hairs (3-5 mm. long), rusty red at maturity, growing inwards from the suture. *Seeds* ovoid, black, bearing streaks of very minute brown fuzz hairs, giving a black and brown striped effect.

It is curious that no one seems to have observed that the characteristic rusty red hairs occupying a large part of each loculus in the capsule develop from the capsule sutures and not from the seed. Watt (1907, pl. 51) even illustrates the seed 'showing floss'. His illustration (same plate) of the seed '(floss removed)' shows all the hair that actually grows from the seed coat.

DISTRIBUTION. Coastal Kenya, coastal sands and dry hills in eastern Tanganyika, coastal sands in Portuguese East Africa and northern Natal.

(2) *G. brevilanatum* (Hoch.) J. B. Hutchinson comb.nov. (Syn. *Gossypium brevilanatum* Hoch. (1925)). *Chromosome* number $2n=24$. Perennial, woody, subscandent *shrub*. *Stems*, *pedicels* and *petioles* ribbed, but not winged, very finely pubescent. *Fruiting branches* 2 or more jointed. *Leaves* large, cordate, $\frac{2}{3}$ -palmatifid into 3-7, usually 5, lobes. *Nectaries* on the main veins below the level of the leaf sinuses. *Stipules* small, falcate, persistent. *Bracteoles* small (2 cm. or less), persistent, narrowed to the base, with about 6 teeth along the upper margin. *Petals* greatly exceeding the bracteoles in length, deep golden yellow. *Staminal column* long, antheriferous throughout. *Filaments* very short, the upper ones rather longer than the lower. *Anthems* compactly arranged. *Stigmas* free, separated, but not usually wide spreading. *Capsules* about 35 mm. long and 20 mm. broad, with 5 loculi, hairs on the sutures few and inconspicuous, projecting between the two rows of seeds, 8 or 9 seeds per loculus. *Seeds* covered with a single coat of fine, strongly adherent, light brown, convoluted hairs about 12 mm. long.

DISTRIBUTION. *G. brevilanatum* was collected in Madagascar, where it is endemic, by M. Perrier de la Bathie. It appears to be rare. The living types in the collection at the Cotton Research Station, Trinidad, were grown from seed supplied by Prof. Aug. Chevalier, of the Musée d'Histoire Naturelle in Paris (Hutchinson, 1943).

The two species are genetically completely isolated by a sterility barrier. Capsules of

G. kirkii develop to some extent when pollinated by *G. brevilanatum*, but are always shed within about two weeks of flowering, and the ovules show no sign of growth (Hutchinson, 1943).

Since the morphological differences between them are large, and their chromosome complements are cytologically distinct (Hutchinson, 1943) the existence of the sterility barrier is not unexpected. There is also, however, evidence of a sterility barrier within the species *G. kirkii*. Two types have been cultivated at the Cotton Research Station, Trinidad. The strain studied by Harland and Skovsted (W8-2A) was collected by E. Brand, Esq., of the Tanganyika Department of Agriculture, on the Makonde Plateau, Lindi Province, Tanganyika Territory. It is a strongly growing shrub, almost glabrous on the young parts, with winged stems, and it matches specimens in the Amani (East Africa) herbarium bearing the manuscript name *Gossypium bussei* Gurke. More recently a strain (W8-2B) was established from seed collected in the coastal regions of Kenya by D. E. Edwards, Esq. Plants of this strain are smaller and much less bushy when grown in Trinidad. They are finely hairy and have angled stems. The Kenya plant resembles specimens labelled *Gossypium kirkii* in the Amani herbarium.

Masters's type of the species was collected near Dar es Salaam. The Amani herbarium material which is labelled *Gossypium kirkii* was collected from the region of Dar es Salaam, Handeni, east Usambaras, and Mafia Island in Tanganyika, Pemba in the Zanzibar Protectorate and in coastal Kenya. I am indebted to Mr P. J. Greenway for the information that the Amani specimens labelled *Gossypium bussei* were collected in the Lindi and Kilwa districts in south Tanganyika where also Brand's type was obtained. The southernmost record of the species is by Bowmaker from northern Natal and his specimens agree with Brand's Makonde Plateau material. Nevertheless, there is no definite association between morphological characters and geographical distribution. A specimen from between Vila Joao Belo and Inharrime (Portuguese East Africa) in the Pretoria herbarium resembles the Kenya form in some characters, and living plants grown at Barberton (Transvaal) from a stock derived from southern Tanganyika were more like the *G. kirkii* of the Amani collection than the *G. bussei* material.

Although herbarium material from wild plants cannot be classified with confidence into two types, the two strains in the Trinidad collection, W8-2A and W8-2B, only cross with difficulty. Of 56 flowers of W8-2A pollinated by W8-2B, 55 were shed within two weeks. (A parallel set of flowers of W8-2A was emasculated and pollinated with self pollen, and about half the flowers set and gave capsules that yielded normal seed.) In most cases the capsules developed to some extent, but no sign of ovule development was to be seen at that time of shedding. One capsule developed normally and contained three seeds, two of which were empty. One hybrid plant was obtained, which resembled the female parent closely. It set freely, but the capsules contained less than 70% of the normal complement of seeds. Batches of seed of each of the parent species and of the F_1 were sown together for comparison, and records of germination taken. The following results were obtained:

Type	Seeds sown	Germinated	Died	Percentage viable
W8-2A	100	52	48	52
W8-2B	11	7	4	64
F_1	100	16	84	16

The low set in the F_1 capsules and the poor germination of seed from the F_1 plant suggest that the parent types are widely different in genetic constitution in spite of their morphological similarity.

Genetic differentiation of this magnitude is usually associated with a true species of difference. Since the two forms cannot be distinguished morphologically, however, there can be no justification for recognizing more than the one species (*G. kirkii*). Re-examination of the species in the field is much to be desired, to discover whether an ecological or geographical isolation barrier exists, behind which genetic differentiation could have gone on.

Whether or not morphological differences between the two forms are ultimately demonstrated, it is evident that genetic differentiation has gone on faster than morphological separation, a state of affairs that has rarely been recorded in plants except as a consequence of polyploidy. In this respect the genetic situation in *G. kirkii* resembles that of certain species of *Drosophila* (Dobzhansky, 1941), which were in the first instance separated by the differences observed between their germ plasms, and were only later shown to be distinct in habitat and ecology.

The genus *Thespesia*

Thespesia Corr., Montezuma Sess. & Moc., *Maga* Urban, *Armouria* Lewton, *Azansa* Alef., *Shantzia* Lewton. Chromosome number $2n=26$ (wherever known). Shrubs or trees 1-15 m. tall. Leaves entire or broadly 3-5-lobed. Flowers solitary and axillary on simple pedicels, or on jointed peduncles, or borne several together on sympodial fruiting branches. Involucral bracteoles 3-15, free, ovate acute or acuminate, linear, or filiform, often small, persistent or caducous. Calyx usually truncate, 5-pointed, sometimes drawn out into long teeth, persistent or circumscissile. Anthers unilocular, arranged on short filaments arising from a staminal column. Stigmas united, clavate. Capsules leathery or woody, indehiscent or tardily dehiscent, sometimes dry and brittle and loculicidally dehiscent. Seeds turbinate or obovoid compressed, naked or fuzzy.

The type of the genus is *Thespesia populnea* Solander.

Eight species are recognized here. The three Antillean species (*T. grandiflora*, *T. cubensis* and *T. beata*) and the East African *T. danis* form a natural group with the circumtropical, shore-loving *T. populnea*. The African *T. garckeana* and the Asiatic *T. lampas* are very distinct, but are possibly linked with the *T. populnea* group by the Mexican *T. tomentosa* and the Antillean *T. beata*.

The species of *Thespesia* may be distinguished as follows:

- | | |
|--|----------------------------|
| a. Involucral bracteoles 3—b. | |
| b. Leaves glabrous, or finely lepidote below—c. | |
| c. Calyx persistent—d. | |
| d. Involucral bracteoles small, caducous. | 1. <i>T. populnea</i> . |
| dd. Involucral bracteoles large, persistent. | 2. <i>T. danis</i> . |
| cc. Calyx circumscissile—e. | |
| e. Flowers large, rose pink. | 3. <i>T. grandiflora</i> . |
| ee. Flowers small, yellow. | 4. <i>T. cubensis</i> . |
| bb. Leaves stellate tomentose below. | 5. <i>T. beata</i> . |
| aa. Involucral bracteoles 4-15—f. | |
| f. Involucral bracteoles arranged in 3 groups—g. | |
| g. The whole plant stellate tomentose. | 6. <i>T. tomentosa</i> . |
| gg. Plant sparsely hairy or almost glabrous. | 7. <i>T. lampas</i> . |
| ff. Involucral bracteoles evenly spaced. | 8. <i>T. garckeana</i> . |

Three species formerly assigned to the genus are here excluded. Of *T. brasiliensis* Spreng., the description is inadequate, but the paniculate inflorescence and the serrated leaf margin are not such as would be expected in *Thespesia*. *T. campylosiphon* can be confidently excluded on the arrangement of the stamens on the staminal column. *T. altissima* has been separated by Blume as *Neesia altissima*. It resembles *Kokia* in having a calyx which encloses the bud, but differs from both *Thespesia* and *Kokia* in having capitate stigmas.

(1) *T. populnea* Solander, *T. populneoides*, *T. macrophylla* Blume, *T. populnea* var. *acutiloba* Bak. f. Chromosome number $2n=26$. Small, usually shore-growing tree about 5 m. tall. Leaves ovate acuminate entire, rarely shallowly but acutely 3-lobed, cordate, glabrous and leathery. Flowers yellow, solitary, axillary, borne on simple pedicels. Involucral bracteoles 3, free, small, caducous. Calyx truncate with 5 minute teeth, repand-rotate at maturity. Stigmas united, clavate. Capsules leathery, indehiscent. Seeds obovoid, compressed, covered with a very short brown fuzz.

Several forms have been recorded. The most marked difference is in the length of the pedicels. In the form commonly found in the New World, Africa and western India, the pedicels are much shorter than the petioles (Blume's *T. macrophylla*). All specimens seen from Australia, many of those from Polynesia, the Philippines and Madras and Ceylon, and a few from East Africa, are of a form with long pedicels that are about equal in length to the petioles (Blume's *T. populnea*). In addition to these Roxburgh has separated an Indian form with long acuminate leaves as *T. populneoides*, and Baker a form from Natal and Lorenzo Marques with small, shallowly but acutely 3-lobed leaves as *T. populnea* var. *acutiloba*. None of them appears to be sufficiently distinct to warrant separation as either species or varieties. Specimens in the Kew herbarium from the Dutch East Indies labelled *T. macrocarpa* belong to this species.

DISTRIBUTION. Circumtropical, generally on seashores. The area of greatest variability is the Indian and East African region. The Antillean type resembles the common African rather than the common Polynesian form.

(2) *T. danis* Oliver. Shrub about 6-8 ft. tall. Leaves practically glabrous, very broadly ovate, entire, scarcely to markedly cordate. Flowers yellow, solitary, on simple pedicels in the axils of the upper leaves. Pedicels about equal to the petioles in length, thickened below the flower. Involucral bracteoles 3, borne widely separated on the thickened summit of the pedicel, ovate or ovate-acute, entire, persistent, 1-1.5 cm., rarely up to 3 cm. long. Calyx truncate, 5-pointed. Stigmas united, clavate.

DISTRIBUTION. Somaliland, Tanaland and Mombasa in Kenya, and Tanga, Usambara and Morogoro in Tanganyika.

(3) *T. grandiflora* DC., *Montezuma speciosissima* Ses. & Moc., *Maga grandiflora* Urban. Tree up to 15 m. tall. Leaves large (c. 20 cm. long), ovate acuminate entire, shallowly cordate, glabrous and leathery. Flowers large, rose pink, solitary, axillary on simple pedicels. Involucral bracteoles 3, free, small, caducous. Calyx subcampanulate, truncate with 5 minute teeth, circumscissile after flowering. Stigmas united, clavate. Capsules more or less leathery, indehiscent. Seeds obovoid, compressed, naked.

DISTRIBUTION. Central and western Puerto Rico.

(4) *T. cubensis* (Britton & Wilson) comb. nov. *Montezuma cubensis* Britton & Wilson. Tree up to 15 m. tall. Leaves leathery, 6-12 cm. long, ovate acuminate entire, very deeply cordate, or auriculate, the auricles often overlapping, glabrous above, densely and finely

lepidote beneath. *Flowers* small, brown-yellow, solitary, axillary on simple pedicels. *Involucral bracteoles* 3, free, small, caducous. *Calyx* subcampanulate, truncate with 5 minute teeth, circumscissile after flowering. *Staminal column* about twice as long as the petals. *Stigmas* united, clavate. *Capsules* more or less leathery, indehiscent. *Seeds* obovoid, compressed, naked.

DISTRIBUTION. Cuba.

(5) *T. beata* (Lewton) comb.nov., *Armouria beata* Lewton. *Tree* 5-7 m. tall. *Leaves* 4-6 cm. long, 3-5 angulate-lobate, cordate at the base, scabridulous above, softly stellate-tomentose below. *Flowers* cream coloured, solitary, axillary on simple pedicels. *Involucral bracteoles* 3, linear lanceolate or trifid, 2-3 mm. long, caducous. *Calyx* cupulate, truncate with 5 minute teeth, persistent, becoming woody and verrucose, but keeping its form. *Stigmas* united, clavate. *Capsules* jointed, ovoid, woody, tardily splitting into 5 woody valves, densely stellate-pubescent externally. *Seeds* obovoid, naked.

DISTRIBUTION. Beata Island, of the south coast of Haiti.

That these three endemic insular species are closely related to *T. populnea* can scarcely be doubted. Their chromosome numbers have not yet been determined, and no attempts at interspecific hybridization have been made, but such investigations would be of great interest and might yield important information on the evolutionary processes leading to the differentiation of insular endemics.

(6) *T. tomentosa* Presl. *Tree* or *shrub*, covered on all parts with a stellate tomentum. *Leaves* cordate, subrotund, broadly entire or 3 angulate-lobate. *Flowers* subsessile, erect. *Involucral bracteoles* 8, arranged in 3 groups, setaceous, tomentose, early caducous, leaving 3 transverse, oblong callosities at the base of the calyx. *Calyx* turbinate campanulate, tomentose, with rounded, obscurely uninerved, mucronulate lobes. *Corolla* twice as long as the calyx, tomentose-velutinous without, reflexed. *Fruit* unknown. (Description from Presl, 1836.)

DISTRIBUTION. Western Mexico.

(7) *T. lampas* Cav., *Hibiscus lampas* Cav., *Azanza lampas* Alef., *T. sublobata* Blanco. *Chromosome* number $2n=26$. *Shrub* 1-2 m. tall. *Leaves* almost glabrous, cordate, entire or broadly 3 angulate-lobate. *Flowers* yellow, borne on jointed peduncles or on 2-5 jointed, sympodial fruiting branches. *Involucral bracteoles* 4-6, arranged in 3 groups, small, filiform, caducous. *Calyx* cup drawn out into 5 long teeth, rarely almost truncate with 5 small teeth. *Capsule* ovoid-angled, drying thin and brittle and dehiscing widely; rarely rather woody and not dehiscing widely (the form described by Dalzell in the Bombay Flora); containing c. 8 seeds per loculus. *Seeds* small, turbinate, black, naked, except for a minute tuft of brown fuzz at the tip.

The chromosome number has been recorded by Skovsted (1940) and has been checked by Dr S. G. Stephens on plants grown in Trinidad from Jamaican seed.

DISTRIBUTION. Ceylon, India, Burma, Siam, Indo-China, the Philippines, Hainan, Java, Celebes, Hawaii, Jamaica.

T. lampas has been spread considerably as an ornamental. It only occurs as a cultivated shrub in Jamaica. Blume states that it was probably introduced into Java from Bengal, and according to Dr Merrill (in a letter to Dr Harland when he was at the Cotton Research Station, Trinidad) it is probably introduced in the Philippines. The area of greatest variability is India, where it is a forest shrub.

(8) *T. garckeana* F. Hoffm., *T. rogersii* Moore, *T. trilobata* Baker f., *T. debeerstii* De

Wild & Th. Dur., *T. hockii* De Wild. Chromosome number $2n=26$. Shrub or small tree 2-10 m. tall, suckering freely when felled. Leaves cordate, usually 3-lobed, rarely entire; lobes usually broad at the base and rounded, sometimes acute; leaf surface rough, usually densely, sometimes sparsely, stellate hairy below. Flowers solitary, borne on jointed peduncles in the axils of the uppermost leaves. Peduncles variable in length, bearing two small caducous bracts at the joint. Involucral bracteoles 9-15, evenly spaced, linear, twice as long as the calyx, usually caducous before anthesis, leaving scars forming a continuous ring round the base of the calyx, sometimes more or less persistent. Calyx truncate, usually with 5 small teeth, persistent. Stigmas united, clavate. Capsules obovoid, ovoid or flattened, woody, opening tardily, hairy on the outside. Seeds obovoid, compressed, covered with a dense, short, rusty brown fuzz.

DISTRIBUTION. Africa, from Kordofan and Equatoria through Kenya, Tanganyika, Nyasaland and the Belgian Congo to the Rhodesias and Portuguese East Africa. The characteristic habitat of the species is rather open bush country, and there is considerable variation in size according to locality. In the tall bush or open forest of Nyasaland, it grows to a tree 10 m. tall. At the other extreme, in dry, open scrub in Maswa, Lake Province, Tanganyika, it rarely exceeds 2 m. The free suckering habit makes it particularly suitable for survival in the face of shifting cultivation and it is consequently common in abandoned cultivations. Variability is greatest in the southern part of the range, the various forms that have been given specific rank by previous authors having been collected chiefly in the Belgian Congo and the Rhodesias.

Considering the genus as a whole, what may be regarded as the two extreme species, *T. garckeana* and *T. danis*, occur side by side in Africa. The greatest diversity of species is to be found in the Central American region. There appears to be no information on *T. tomentosa* beyond the original Latin description, but from Presl's account it is morphologically intermediate between the *T. populnea* group and *T. garckeana* and *T. lampas*. In the *T. populnea* group, all species have 3 bracteoles. All save *T. beata* are glabrous and almost invariably have entire leaves. *T. beata* resembles the *T. garckeana* group in bearing a stellate tomentum, and in having 3 angulate-lobate leaves. *T. tomentosa* is apparently very similar to *T. beata*, but has 8 involucral bracteoles, though in this species and in *T. lampas*, the bracteoles are arranged in groups of three, suggesting homology with the set of three characteristic of the *T. populnea* group. On the whole it seems fair to speculate that the original differentiation of the genus was in the Central American region. Spread into the Old World resulted in the evolution of *T. danis* from the section with entire, glabrous leaves and three bracteoles, and of *T. garckeana* and *T. lampas* from the section with lobed, hairy leaves, and more than three bracteoles. *T. populnea*, which has not developed continental subspecies, was presumably spread at a later date, probably owing its wide dispersal to carriage of the fruits by ocean currents.

Thespesia is evidently closely related to *Gossypium*. Attempts at intergeneric grafting showed that *G. sturtii* will form good graft unions with *Thespesia populnea* and *T. lampas*. All other grafts attempted between the genera failed to form a union. The basic chromosome number in the species of *Thespesia* that have been examined is the same as the basic number in *Gossypium*, and some attempts have been made at the Cotton Research Station, Trinidad, to obtain intergeneric hybrids. Harland (MS. record) found that pollen of *Thespesia populnea* would not grow on stigmas of *Gossypium*. Flowers of a tetraploid race of *G. arboreum* pollinated with either *Thespesia garckeana* or *T. lampas* fell in 6-8 days.

Reciprocal crosses of *T. lampas* × *Gossypium klotzschianum* var. *davidsonii* fell in 3–4 days. On the other hand, of 6 flowers of *G. anomalum* pollinated by *Thespesia lampas*, 4 fell in 5 days but 2 matured, giving empty seeds (Stephens, MS. record). In this case it seems likely that fertilization occurred, but evidently the embryos did not develop far.

The genus *Kokia*

Kokia Lewton. Trees, 12–15 ft. tall. Flowers borne singly in the axils of the upper leaves. Peduncles jointed, bearing a broadly sessile, obliquely clasping, caducous, ovate bract at the joint. Involucral bracteoles 3, persistent, accrescent, ovate entire, sinuate or slightly lobed, narrowed at the base, coriaceous, glabrous. Calyx urceolate, thin, scarious, punctate with black warts; lobes 5, shallow, rounded, the margins overlapping and completely enclosing the bud. Calyx tube often with a median transverse vein, the upper half of the calyx usually soon breaking off at this point, giving the calyx the appearance of being truncate. Corolla twice or thrice the length of the bracteoles, red. Ovary 5-celled, with one ascending ovum in each cell. Capsule ovoid, ligneous, opening tardily. Seeds obovoid, sharply angled on the ventral side, rounded on the dorsal, covered with a short brick-red tomentum. (Description after Lewton.)

The genus is endemic in the Hawaiian Islands. Lewton made three species, and some others have been named since, but the differences between them are small. The whole genus is extremely rare and on the verge of extinction, and material and information on it are so scanty that it is not possible to use the criteria of variability and geographical distribution to assess the value of the species distinctions that have been proposed.

The genus *Notoxylinon*

Notoxylinon Lewton. Established by Lewton to cover Australian species formerly placed in *Cienfugosia* (*Fugosia*). Shrubs or undershrubs. Flowers borne on short sympodial fruiting branches, or jointed peduncles, sometimes with a leafy bract at the joint. Involucral bracteoles 3, small, linear lanceolate or subulate, often caducous. Calyx more or less 5-lobed or 5-parted; oil glands on the calyx scattered. Capsules 3 or 4 locular, loculicidally dehiscent. Seeds usually pubescent or woolly.

Lewton accepted 7 species, all confined to Australia. From his descriptions, the following key was compiled:

- | | |
|--|------------------------------|
| a. Calyx truncate, strongly 5-toothed—b. | 1. <i>N. populifolium</i> . |
| b. Plants glabrous, bracteoles persistent. | 2. <i>N. thespesioides</i> . |
| bb. Plants more or less tomentose, bracteoles caducous—c. | 3. <i>N. flaviflorum</i> . |
| c. Leaves orbicular-ovate, acute, entire: bracteoles subulate. | 4. <i>N. punctatum</i> . |
| cc. Leaves rhomboid, 3-lobed, bracteoles setaceous. | 5. <i>N. latifolium</i> . |
| aa. Calyx 5-parted or deeply lobed, lobes acuminate—d. | 6. <i>N. australe</i> . |
| d. Plants glabrous or slightly tomentose, leaves entire—e. | 7. <i>N. pedatum</i> . |
| e. Petioles less than 1 in. long. | |
| ee. Petioles 1 in. long or more. | |
| dd. Plants hairy—f. | |
| f. Leaves entire or 3-lobed, densely short tomentose. | |
| ff. Leaves pedately 5-parted, coarsely stellate hairy. | |

No adequate material is at present available on which to base detailed species descriptions, or a study of the distribution of variability. There is in the Kew herbarium, however, a note by Sprague on the distribution of these species, and of another (*N. pul-*

chellum) based on information supplied by Gardner. Gardner's data are summarized in the following table:

Species	Territory			
	Western Australia	Kimberley Dist. (N.W.)	Northern Territory	Queensland
<i>N. pedatum</i>				
<i>N. punctatum</i>				
<i>N. thespesioides</i>			
<i>N. australe</i>				
<i>N. flaviflorum</i>				
<i>N. latifolium</i>				
<i>N. populifolium</i>				
<i>N. pulchellum</i>				

There appears to be some uncertainty about the distribution of *N. thespesioides*, concerning which the record states 'probably Northern Territory, or perhaps Kimberley in Western Australia'.

The outstanding feature of these distributions is the extent to which the species are sympatric. Even if detailed studies result in a reduction in the number of species accepted, it does not seem possible that they will fall into allopatric groups. The genus deserves further taxonomic and geographic study, to determine how many of the named species are really distinct, and the nature of the barriers by which they were originally isolated.

The genus *Alyogyne*

Alyogyne Alefeld. Established to cover two Australian species of succulents formerly ascribed to *Cienfugosia* (*Fugosia*). Succulent, glabrous shrubs. Flowers borne on jointed peduncles. Involucre a 5-7 pointed cup inserted 3-5 mm. below the calyx. Calyx deeply 5-parted. Capsule 5-locular. Seeds hairy.

Lewton accepts four species, but from what scanty information is available, there seems no justification for allowing more than two. These may be distinguished as follows:

- | | |
|---|----------------------------|
| a. Leaves entire, cuneate oblong or broadly linear. | 1. <i>A. cuneiformis</i> . |
| aa. Leaves narrow linear or almost terete, most deeply divided. | 2. <i>A. hakeaefolia</i> . |

Sprague (record in Kew herbarium), quoting Gardner, gives the distribution of the two species as follows:

A. cuneiformis. Western Australia, 'Eremaea Province', red sandy areas, Shark Bay: of limited distribution near the coast.

A. hakeaefolia. Western Australia, 'Eremaea Province' and western area of Southern Australia; granitic loamy soils with a rainfall of 25-10 in.

DISCUSSION

It may fairly be claimed that the application of Vavilov's and Mayr's principles has made possible a simple and orderly account of the relationships of species of *Cienfugosia* and *Thespesia*. Moreover, at least as far as these genera are concerned, the two principles are complementary. Accepting continuous variation as intraspecific, all discontinuous (interspecific) variation proves to be associated with geographical separation, either still existing or to be inferred in the past from the distribution of the intraspecific variation. The situation in *Gossypioides* is not so straightforward, since in *G. kirkii* there is evidence of a genetic divergence which is not associated with morphological differentiation. Further

POLLEN COLLECTION BY *APIS MELLIFERA*

By MARY PERCIVAL

(With 18 figures in the text)

INTRODUCTION

The honey bee (*Apis mellifera*) is generally regarded as one of the most important pollinators in the British Isles. Data indicating the extent to which this insect is responsible for pollinating our economically important crops are at the present time being collected at several centres. It was not with this object primarily in view that the present work was undertaken. Although the records show the extent of the bees' activities in this direction, it was with a view to interpreting the relationship between the hive bee and the flora of the neighbourhood that observations were made. The line of approach therefore is that of the floral biologist rather than that of the economic entomologist. This approach entails a study of the insects and the flora and also of the climatic conditions affecting both groups profoundly.

METHOD OF COLLECTING DATA ON THE HONEY BEE

It was decided that the most informative datum of the bees' activities that a single observer could collect would be that of the pollen income. As only one hive of bees was available, a pollen trap could not be used on it, as the colony would have starved. In addition, it was felt that to use a trap, since it would have deprived the bees of their pollen loads, would have introduced an added unknown factor in the pattern of their environment. The method adopted was to record the number of bees laden with pollen as they alighted on the flight of the hive, classifying the loads as to colour and texture on a chequer-board marking sheet. The distribution of the pollen on the bee's body was also noted and proved a valuable aid in separating pollens of somewhat similar colour. Recordings were made for ten periods of 35 min. each during the day, beginning at 8 a.m. G.M.T. and finishing at 5.35 p.m. In the intervals between recordings, sample pollen loads were taken from incoming bees and meteorological observations, such as were not automatically recorded, were taken. Notes were also made of the general activity of the bees including the emergence of orientation flights.

METHOD OF COLLECTING DATA ON THE FLORA

One day was set aside each week for listing the constituents of the flora and noting the relative abundance of the species. A floral map was constructed each week for the whole of the land within $\frac{1}{2}$ -mile radius of the hive. The map showed the distribution and abundance of the major species only, but all species in flower were recorded in the notes. Peaks in the blooming of individual species were noted when they occurred. A record was kept of the dates of agricultural operations, such as hay and corn cutting, harrowing, hoeing or grazing of crops, since these were likely to affect the distribution or quantity of species in flower.

METEOROLOGICAL DATA

Temperature was recorded by an electric thermograph, installed in a Stevenson screen 5 yd. from the hive. Sunshine was recorded by means of a Jordan's sunshine recorder. Air movements were recorded by means of a Metrovic velometer. The time and duration of rainfall was noted, but no measurements were taken of the amount of precipitation.

DURATION OF OBSERVATIONS

Observations began on 28 April and finished on 23 August 1945. This period covers the main part of the active season of the colony.

PLACE OF OBSERVATIONS

Ty Mynydd, Radyr, Cardiff, South Wales. Within the $\frac{1}{2}$ -mile radius the geological formation is chiefly red marl at an elevation of 200-300 ft., dropping by 100 ft. to the alluvium of the Taff Valley. The higher land consists of pastures and hayfields with small areas of arable land under cereals and roots. The alluvium is intensively cultivated with market-garden crops (Fig. 4).

POPULATION OF HIVE BEES

Within the area were twenty-one colonies. Two only were at Ty Mynydd. The main concentration was that of eleven stocks, eight strong and three weak, on the edge of the bean fields in the Taff Valley. The positions and numbers of the stocks are shown in the map.

NOTES ON THE COLONY AND HIVE MANIPULATIONS

The colony of bees was brought from a seaside district (Newton, Porthcawl), a distance of 18 miles to Radyr, on 25 April, i.e. 4 days before observations began. The bees were 'British' bees with both black and yellow banded workers. The bees covered nine frames and were put into a w.b.c. hive. The brood chamber was completed with a frame of drawn comb. There was a great deal of sealed brood but very little unsealed, and only a small amount of honey at the tops of the combs. As the stores were so short, a queen excluder was put over the brood chamber and a super of shallow frames, containing about 15 lb. of honey was placed above it. This honey was chiefly collected from blackberry and white clover in the 1944 season. As neither of these species is spring flowering no risk was run of 'conditioning' the bees to any element of the spring flora. A tube containing methyl salicylate was placed in the brood chamber as a precaution against acarine disease. Throughout the season the hive had the minimum of manipulations necessary for its welfare. A brief account of them is given below. The colony did not swarm.

Manipulations of Hive. 23 April-23 August

25. iv. 45. Super containing 15 lb. honey placed above brood chamber.
23. v. 45. The super given on 25 April had seven frames full of honey and one empty frame. A second super of eight shallow frames of drawn comb placed above it.
24. vi. 45. The second super had $6\frac{1}{2}$ frames of honey and also contained some pollen and false queen cells. A third super of drawn comb was placed above the second.

29. vi. 45. The third super was more than half-full of honey. Tube containing methyl salicylate placed in it.

5. vii. 45. Hive examined. There was a great deal of sealed brood in the brood chamber but only a small amount of unsealed brood and pollen. A few half-formed queen cells found and destroyed. Several bees seen with dislocated wings so acarine disease suspected. Four tubes containing methyl salicylate placed in brood chamber. The three supers were only half-full of honey.

25. vii. 45. Super clearer placed beneath the two upper supers.

28. vii. 45. Two upper supers removed and super clearer placed beneath remaining super. Four frames of second super were one-quarter to one-third full of pollen.

5. viii. 45. Remaining super removed and an empty extracted super replaced to accommodate the bees.

7. viii. 45. Brood chamber was not well provided with stores so the last super to be removed was replaced intact with its honey, above the brood chamber. A clearing board, with the trap open, was placed above it. The two extracted supers were placed on top for the bees to clean. The yield of surplus honey was 43 lb.

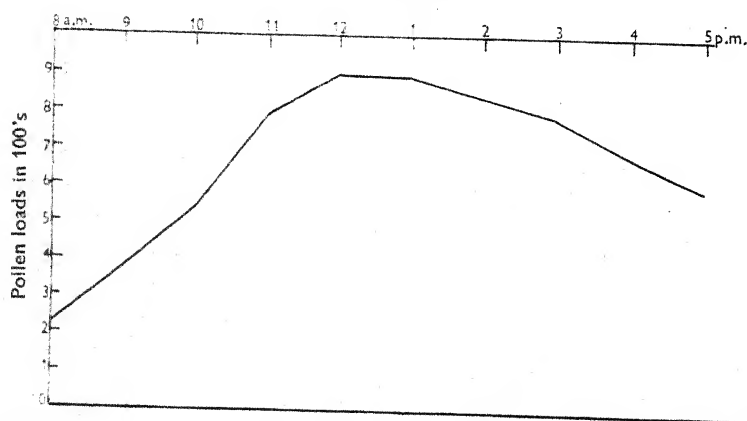


Fig. 1. Daily rhythm of pollen collection. Graph of the average number of pollen loads counted per 35-min. period from 8 a.m. to 5.35 p.m. for 28 April to 23 August.

FINDINGS ON THE POLLEN INCOME AND FLORAL DATA

Pollen collection: takes place throughout the day if weather conditions permit. The rhythm of pollen collection during the day is a curve with maximum values between 12 noon and 1.30 p.m. (Fig. 1). As the daily curves showed violent fluctuations due to changeable weather conditions, the curve was constructed from the average hourly figures for the whole period 28 April–23 August. The high values between 4 and 5.35 p.m. are caused by most of the bees returning with their last loads of pollen for the day. After 5.30 p.m. the curve falls rapidly to zero. Virtually no pollen is brought in before 8 a.m. probably because the humidity is too high to permit pollen presentation in most species.

Daily pollen income. The number of pollen loads brought in each day varied greatly owing to changeable weather conditions. An examination of Fig. 2 shows that the greatest amount of pollen is collected at the time at which the major nectar crops are in flower, and that peak days in pollen collection coincide with peaks in the flowering of the

major crops. Illustrating this latter point, on 6-7 May the weather became suddenly warm after a notably stormy and frosty period. The hawthorn (*Crataegus monogyna*), burst into bloom and reached a peak by the afternoon of 7 May. This is reflected in the pollen graph. The first peak in the flowering of *Rubus fruticosus* coincided with the flowering of *Trifolium repens*. Over this period, 18 June-17 July, pollen income was greatest. A second peak in the flowering of *Rubus fruticosus* occurred 23 July-1 August and this is also reflected in the pollen-income curve. After four stormy days, 5-8 August, the blackberry had nearly finished flowering and there was little left for the bees but

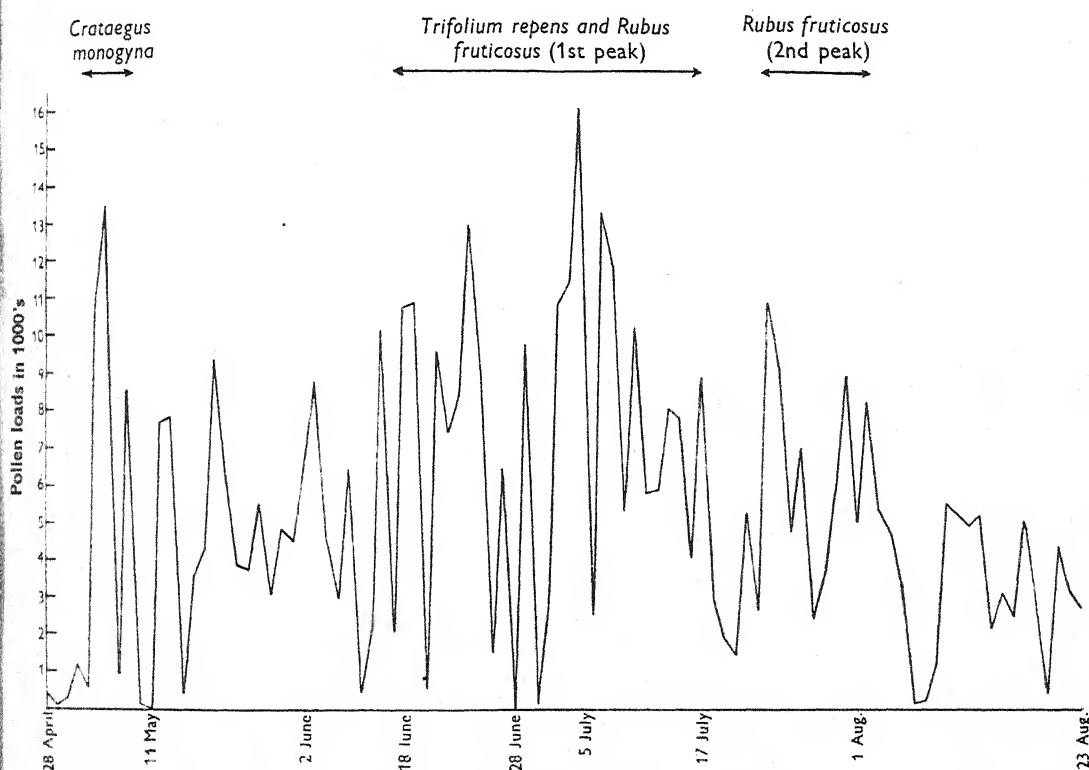


Fig. 2. Daily pollen income for period 28 April-23 August. The daily totals represent the number of loads counted during the observational periods and require to be doubled to obtain the total income. The peak periods of the flowering of three major crops are shown.

Clematis vitalba and a little second crop *Sinapis arvensis* (Charlock) and *Raphanus raphanistrum* (Wild Radish). These were fully exploited but the pollen income remained low. It was at this time (8-12 August) that the bees brought in nearly 3000 loads of spores of an unidentified rust fungus. A lean period, the so-called 'June-gap', occurred between the end of the flowering of the raspberry (*Rubus idaeus*) and the opening of the blackberry and clover (7-18 June). The bees used up a whole 'super' of honey (about 20 lb.) collected from the raspberry, but the pollen income was fairly well maintained by *Cornus sanguinea*, *Sambucus nigra*, *Hypochaeris radicata* and *Vicia faba*.

The coincidence of periods of maximum pollen collection and the flowering of major elements of the flora is in accordance with the findings of Todd & Bishop (1941).

Table 1. Species analysis of daily pollen income. Major pollen sources

	<i>Brassica oleracea</i> (vars.)	<i>Crataegus monogyna</i>	<i>Ranunculus bulbosus</i>	<i>Sarcobatus</i>	<i>Vicia faba</i>	<i>Sambucus nigra</i>	<i>Rubus idaeus</i>	<i>Cornus sanguinea</i>	<i>Hypochaeris radicata</i>	<i>Smilax acensis</i>	<i>Trifolium repens</i>	<i>Rubus fruticosus</i>	<i>Castanea sativa</i>	<i>Ephedra angustifolia</i>	<i>Heracleum sphondylium</i>	<i>Centaurea nigra</i>	<i>Raphanus raphanistrum</i>	<i>Clematis italica</i>	<i>Tenacium scordonia</i>	<i>Alnus plantagin-</i>
April 28	22	262	16	44																
29	14	50	3	3																
30	123	180	25	26																
May 1	123	484	303	140																
2	90	273	128	73																
6	905	5520	390	3835																
7	492	10438		2420																
10	38	527		308	59		9													
12	141	6509		949	263		518													
13	141	5		14	2		130													
14	197	1	1	3			8													
15	186	3390	23	1264	275	65	2449													
16	186	2161	16	995	787	58	3596		14											
19			2	97	7		287		21	1										
20		145	71	1014	1275	44	852		30	63										
21		110	146	1006	290	56	2319		142	102										
22			236	1977	1018		5468		291	110										
23		81	112	2580	1922	33	1342		36	110										
24			10	1301	995	9	1244		39	29										
26			45	212	534	76	2537		262	39	1									
27			264	377	934	407	2993		375	97	5									
28			16	588	303	340	1624		82	76	10									
29			138	986	618	331	2473		59	130	9									
31			133	271	231	270	3071		337	117	3									
June 2			167	428	654	425	3693	244	591	112	30									
4			224	190	1299	623	3504	1804	305	135	102									
7			74	3	160	306	1234	1598	674	44	173									
9					214	122	211	1611	216	31	192									
13			143		440	947	424	630	1512	344	1535	150								
14			3		4	15		308		22	3	6								
15			90		140	109		406		35	420	100								
16					426	1319	16	419	2030	1626	2105	1222								
17						146	85			695	81	415								
18							170	111	1661	918	5138	2214		6						
19					307				935	720	5288	3773		15						
20									343	76	24	106		12						
21							43		520	449	4940	3452		15						
22									653	299	3007	3275		10						
23									554	222	3771	3599		19						
24									702	229	6860	4978		9						
25									193	114	986	2057		6						
26									48	47		277								

27	28	29	30	31	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
251	3	201			1																						
3566	16	5205	3016	97	1167	4460	7256	2957	8397	1283	131	334	723	127	142	105	75	106	85	110	3	31	25	461	35	7	
2176	3016	97	1167	388	480	5254	2957	559	144	228	131	334	723	127	142	105	75	106	85	110	3	31	25	461	35	7	
20	4	827	27	388	480	5254	2957	559	144	228	131	334	723	127	142	105	75	106	85	110	3	31	25	461	35	7	
12	1	67	15	115	147	14	26																				
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251	3	201			1																						
3566	16	5205	3016	97	1167	4460	7256	2957	8397	1283	131	334	723	127	142	105	75	106	85	110	3	31	25	461	35	7	
2176	3016	97	1167	388	480	5254	2957	559	144	228	131	334	723	127	142	105	75	106	85	110	3	31	25	461	35	7	
20	4	827	27	388	480	5254	2957	559	144	228	131	334	723	127	142	105	75	106	85	110	3	31	25	461	35	7	
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251	3	201			1																						
3566	16	5205	3016	97	1167	4460	7256	2957	8397	1283	131	334	723	127	142	105	75	106	85	110	3	31	25	461	35	7	
2176	3016	97	1167	388	480	5254	2957	559	144	228	131	334	723	127	142	105	75	106	85	110	3	31	25	461	35	7	
20	4	827	27	388	480	5254	2957	559	144	228	131	334	723	127	142	105	75	106	85	110	3	31	25	461	35	7	
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Table 3. *Species from which pollen was collected from 28 April to 23 August 1945**A* = crop abundant.*LA* = locally abundant.

Number = no. of individuals of tree species.

Asterisks denote pronounced discrepancies between columns 3 and 4.

		Number of loads of pollen recorded	Duration of flowering	Period of exploitation by bees for pollen	Time of day of pollen collection
Major sources of pollen					
<i>Trifolium repens</i>	<i>A</i>	135,694	24. v-23. viii	26. v-23. viii	9 a.m.-5.30 p.m.
<i>Rubus fruticosus</i>	<i>A</i>	128,678	31. v-23. viii*	9. vi-23. viii	8 a.m.-5.30 p.m.
<i>R. idaeus</i>	<i>A</i>	40,300	10. v-21. vi	10. v-21. vi	8 a.m.-5.30 p.m.
<i>Sinapis arvensis</i>	<i>LA</i>	31,922	19. v-23. viii	19. v-3. vii	9 a.m.-5.0 p.m.
<i>Crataegus monogyna</i>	<i>A</i>	30,146	28. iv-26. v	29. v-23. viii	9 a.m.-5.30 p.m.
<i>Sorothamnus scoparius</i>	<i>A</i>	21,194	28. iv-3. vii*	28. iv-22. v	9 a.m.-5.30 p.m.
<i>Hypochaeris radicata</i>	<i>A</i>	16,018	16. v-23. viii	28. iv-7. vi	9 a.m.-2.0 p.m.
<i>Vicia faba</i>	<i>A</i>	13,135	10. v-5. vii*	16. v-23. viii	9 a.m.-1.0 p.m.
<i>Epilobium angustifolium</i>	<i>A</i>	9,055	13. vi-23. viii	10. v-18. vi	12 noon-5.0 p.m.
<i>Raphanus raphanistrum</i>	<i>LA</i>	8,566	7. vii-23. viii	18. vi-23. viii	8 a.m.-5.30 p.m.
<i>Cornus sanguinea</i>	<i>LA</i>	7,111	26. v-19. vi	7. vii-23. viii	9 a.m.-5.30 p.m.
<i>Heracleum sphondylium</i>	<i>A</i>	6,895	1. vii-23. viii	2. vi-18. vi	9 a.m.-1.0 p.m.
<i>Castanea sativa</i>	<i>I</i>	5,757	27. vi-14. vii	1. vii-23. viii	8 a.m.-12.0 noon
<i>Sambucus nigra</i>	<i>A</i>	5,611	15. v-5. vii*	27. vi-14. vii	8 a.m.-5.0 p.m.
<i>Centaurea nigra</i>		5,470	9. vii-23. viii	15. v-17. vi	9 a.m.-2.0 p.m.
<i>Clematis vitalba</i>	<i>LA</i>	4,975	25. vi-23. viii	9. vii-23. viii	10 a.m.-5.0 p.m.
				16. vii-23. viii	8 a.m.-4.0 p.m.
Minor sources of pollen					
<i>Ranunculus bulbosus</i>	<i>A</i>	2,835	28. iv-25. vi*	28. iv-16. vi	9 a.m.-4.0 p.m.
<i>Brassica oleracea</i> vars.		2,208	28. iv-16. v	28. iv-16. v	9 a.m.-5.0 p.m.
<i>Prunus lusitanica</i>	<i>I</i>	1,771	4. vi-21. vi	4. vi-19. vi	9 a.m.-5.0 p.m.
<i>Cirsium arvense</i>	<i>A</i>	1,765	25. vi-23. viii*	9. vii-16. viii	8 a.m.-12.0 noon
<i>Teucrium scorodonia</i>		1,761	25. vi-9. viii*	12. vii-1. viii	8 a.m.-5.0 p.m.
<i>Buddleia variabilis</i>		1,731	28. vi-5. viii	28. vi-5. viii	9 a.m.-5.0 p.m.
<i>Alisma plantago</i>	<i>LA</i>	1,660	24. v-21. viii*	10. vii-21. viii	11 a.m.-1.0 p.m.
<i>Plantago lanceolata</i>	<i>A</i>	1,107	28. iv-23. viii	28. iv-11. viii	8 a.m.-5.0 p.m.
<i>Helianthemum chamaecistus</i>		806	16. v-23. viii	16. v-23. viii	8 a.m.-1.0 p.m. (occasionally p.m.)
<i>Ligustrum vulgare</i>		780	12. vi-2. viii*	24. vi-30. vii	8 a.m.-5.0 p.m.
<i>Sparganium ramosum</i>		730	1. viii-23. viii	1. viii-23. viii	8 a.m.-5.0 p.m.
<i>Ulex gallii</i>		716	27. vii-23. viii*	10. viii-23. viii	10 a.m.-1.0 p.m.
<i>Impatiens roylei</i>		532	9. vii-23. viii	9. vii-23. viii	8 a.m.-5.0 p.m.
<i>Hypericum spp.</i>		468	19. vi-23. viii	27. vi-17. viii	8 a.m.-12.0 noon
<i>Tilia europea</i>	<i>3</i>	318	19. vi-5. vii	22. vi-5. vii	8 a.m.-3.0 p.m.
<i>Polygonum persicaria</i>	<i>LA</i>	298	25. vi-23. viii*	12. viii	1 a.m.-2.0 p.m.
<i>Lotus corniculatus</i>		229	10. v-27. vii*	9. vi-26. vi	9 a.m.-5.0 p.m.
<i>Diervilla japonica</i>		207	3. v-28. vi*	22. vi-28. vi	8 a.m.-5.0 p.m.
<i>Mentha spp.</i>		196	9. vii-23. viii	9. vii-12. viii	10 a.m.-2.0 p.m.
<i>Filipendula ulmaria</i>		190	18. vii-23. viii	27. vii-23. viii	8 a.m.-4.0 p.m.
<i>Taraxacum officinale</i>	<i>A</i>	170	28. iv-28. vii	1. v	9 a.m.-12.0 noon
<i>Phaseolus multiflorus</i>		164	4. vii-23. viii	18. vii-30. vii	8 a.m.-11.0 a.m.
<i>Aconitum sp.</i>		146	28. vi-23. viii*	6. viii-23. viii	8 a.m.-10.0 a.m.
<i>Papaver orientale</i>		129	10. v-19. vi	21. v-19. vi	8 a.m.-11.0 a.m.
Composites (mixed)		126			
Umbellifer, unknown		116		9. viii-23. viii	8 a.m.-12.0 p.m.
<i>Aegopodium podagraria</i>		104	12. v-4. vii	21. v-13. vi	9 a.m.-12.0 noon
<i>Campanula spp.</i>		97	3. v-10. vii	7. vi-21. vi	8 a.m.-5.0 p.m.
<i>Aesculus hippocastanum</i>	<i>3</i>	94	28. iv-16. v	28. iv-16. v	8 a.m.-5.0 p.m.
<i>Ilex aquifolium</i>		93	28. iv-15. v	7. v-12. v	9 a.m.-2.0 p.m.
<i>Oenothera biennis</i>		92	4. vii-17. viii	27. vii-17. viii	8 a.m.-2.0 p.m.
<i>Trifolium pratense</i>		66	2. vi-23. viii*	26. vi	5 p.m.-5.30 p.m.
<i>Calystegia sepium</i>		65	18. vii-23. viii	22. vii-8. viii	8 a.m.-12.0 noon
<i>Rhododendron ponticum</i>	<i>LA</i>	64	30. iv-25. vi	30. iv-2. v	9 a.m.-12.0 noon
				27. v-4. vi	9 a.m.-4.0 p.m. (June)
<i>Sorbus aucuparia</i>		52	28. iv-8. v	6. v	9 a.m.-10.0 p.m.
<i>Montbretia pottii</i>		51	18. vii-23. viii	30. vii-8. viii	9 a.m.-11.0 a.m.

Table 3 (continued)

	Number of loads of pollen recorded	Duration of flowering	Period of exploitation by bees for pollen	Time of day of pollen collection
Minor sources of pollen (continued)				
<i>Cheiranthus cheiri</i>	42	28. iv-1. vi*	7. v	12 a.m.-1.30 p.m.
<i>Eupatorium cannabinum</i>	28	18. vii-23. viii	29. vii-5. viii	10 a.m.-12.0 noon
<i>Ranunculus acris</i>	27	2. v-9. viii	7. v-14. vi	9 a.m.-11.0 a.m.
<i>Scilla non-scripta</i>	27	28. iv-20. v	28. iv-6. v	9 a.m.-4.0 p.m.
<i>Allium ursinum</i>	20	28. iv-14. v	6. v	12 a.m.-12.30 p.m.
<i>Cirsium palustre</i>	18	25. v-1. viii*	16. vi-18. vi	9 a.m.-5.0 p.m.
<i>Salvia</i> sp.	17		29. vii-5. viii	8 a.m.-5.0 p.m.
<i>Digitalis purpurea</i>	15	1. vi-4. vii	15. vi	11 a.m.-5.0 p.m.
<i>Melilotus arvensis</i>	14		14. vii	2 p.m.-5.0 p.m.
<i>Deutzia gracilis</i>	13	30. iv.-20. v	30. iv	10 a.m.-1.0 p.m.
<i>Silene cucubalus</i>	12	1. vi-15. vi	7. vi	12 a.m.-12.30 p.m.
<i>Kentranthus ruber</i>	11	18. v-23. viii	29. vi-2. vii	8 a.m.-1.0 p.m.
<i>Rubus loganobaccus</i>	10	2. v-6. vi	12. v	1 p.m.-1.30 p.m.
Unidentified (mixed)	3,458			
Mixed loads of pollen	256			
Rust fungus spores	1,488		4. viii-18. viii	9 a.m.-5.0 p.m.

Sarothamnus scoparius were also present in great abundance and were used as pollen sources in preference to the buttercup, plantain and bluebell. No single factor can account for this preference. The *Crataegus* may have had a higher nectar concentration than the *Ranunculus*, which might explain the relative popularity of these two species, but it is by no means certain that nectar was generally present in the hawthorn in the 1945 season at Radyr. *Sarothamnus* has no nectar but it has very abundant pollen and this may be significant. The matter is discussed later. The neglect of *Scilla* and *Plantago* is unexplained. The main stand of *Scilla* and *Sarothamnus* was 11 acres of waste land, north of the hive, from which the timber was removed in 1940. In 1943-4, *Scilla* was worked by the bees but it was noted that many of them were taking nectar by alighting on the backs of the flowers and inserting their tongues between the bases of the petals. This illegitimate mode of exploitation would mean that no pollen would be collected, and might account for the apparent neglect of *Scilla*. It is more likely that the top canopy of *Sarothamnus*, whose flowers are dry before those of the bluebell in the morning, conditioned the bees to fly at a higher level and that this is the real reason for the neglect of *Scilla*. Evidence in support of this explanation is forthcoming from the observations on mixed pollen loads (see later) where it is found that mixed loads are collected from contiguous plants which have their flowers at the same level. The dearth of *Cirsium* pollen later in the year is explained from the fact that in this neighbourhood the great majority of the plants are female.

Species which were locally abundant were also well worked for pollen, but again there are exceptions. Only a few loads were collected from *Taraxacum officinale*, *Polygonum persicaria*, *Tilia europaea*, *Aesculus hippocastanum* and *Rhododendron ponticum*. The reason for the neglect of *Taraxacum* and *Aesculus* is that when they were in flower (24 April-5 May) the weather was so cold that the bees did not reach the fields in which the former grew, and the trees of the latter were too exposed in the strong cold winds of that period. *Polygonum persicaria* has very scanty pollen which is apparently why the bees worked it chiefly for nectar.

Tilia flowered during the peak period of *Trifolium repens* and *Rubus fruticosus*, when nearly all the bees were working these species for nectar and pollen; and the assumption is that the nectar concentration of *Tilia* was less than that of these two dominants. The reason for its neglect cannot be that the pollen is scanty, for Hyde & Williams (1945) have shown that the pollen production of *T. cordata* is on a par with that of the anemophilous *Quercus petraea*. That the *Tilia* was worked at all was probably due to the weather. The 22 June, when *Tilia* pollen was first brought in, was a dull, cold, windy day, when the bees were unable to forage very far from home. Two of the *Tilia* trees stand protected from the wind near the hives and the bees reached them. After this, for 3 days, a little pollen was collected from them but thereafter they were again deserted even by the nectar gatherers.

The neglect of *Rhododendron ponticum* seems to have been due to competition by *Crataegus* and *Rubus idaeus*, the raspberry providing a 'nectar flow' at the time and attracting nearly all the bees. It does seem that if a good and abundant nectar source is available the bees will make it a chief source of pollen as well.

PLANTS FROM WHICH NO POLLEN WAS COLLECTED

Table 4 shows species growing within the $\frac{1}{2}$ -mile radius of the hive, from which no pollen was collected. Plants known to receive visits from honey bees (either for nectar or pollen) are noted, and those species which formed stands are marked with an asterisk. Those which furnished only scanty pollen *per flower form* are marked S.

There were 227 species in this class. Of these, 202 formed only very minor elements of the flora. They were either single plants in gardens or very thinly dispersed as individual plants in hedgerow and field. The species marked with an asterisk formed stands locally; all these except *Bellis perennis*, *Crepis taraxacifolia*, *Hieracium murorum*, *Rhinanthus crista-galli*, *Rumex acetosa*, *Fagus sylvatica*, *Philadelphus coronarius*, *Solanum lycopersicon*, *Vitis vinifera*, *Pinus sylvestris* and *P. montezumae* were outside the $\frac{1}{4}$ -mile radius.

All but sixty-seven of these species are known to be visited by bees and from eighty-three of them, pollen is known to be collected, so these are potential pollen sources. They include flowers which vary vastly in floral type. They include the wind-pollinated *Fagus*, humble bee and butterfly flowers such as *Antirrhinum* and *Lychnis*, and the shallow-flowered inflorescences of *Anthriscus*. It would seem therefore that there is no type of flower which the honey bee will not visit, other things being equal.

The only things which these plants have in common in the neighbourhood analysed here are: (a) they are very sparsely distributed; (b) they form stands, but the nearest individuals are more than a $\frac{1}{4}$ -mile distant from the hive. In this latter case it is thought that the bees never find the flowers and that this is due, partly to the distance and partly to the fact that most of the species grew to the west or north-west of the hive, so the bees would have had to fly against the prevailing wind to reach them. (The effect of air movement on foraging is indicated in the section on weather.) In the former case it seems that the influence of the major elements of the flora dominates and that the abundant species are selected in preference to the sparse.

For species forming stands within the $\frac{1}{4}$ -mile limit the explanation given above will not suffice. It was thought that pollen would have been collected from the *Bellis-Pinus* group (see list above).

Table 4. *Species from which no pollen was collected*

Family	Species	Known to receive visits from honey bee	Pollen collection observed
Ranunculaceae	* <i>Anemone nemorosa</i>	+	+
	<i>A. japonica</i>	.	.
	<i>Ranunculus lingua</i>	.	.
	* <i>R. flammula</i>	+	.
	<i>R. ficaria</i>	+	+
	* <i>Caltha palustris</i>	+	+
	<i>Aquilegia</i> (cultivated)	+	+
	<i>Delphinium</i> (cultivated)	+	.
	<i>Paeonia</i> (cultivated)	+	+
	<i>Nigella damascena</i>	+	+
	<i>Berberis candidula</i>	+	.
Berberidaceae	<i>B. darwinii</i>	+	+
Nymphaeaceae	<i>Nymphaea alba</i>	+	+
Papaveraceae	<i>Papava nudicaule</i>	+	+
Fumariaceae	<i>Corydalis lutea</i>	+	+
Cruciferae	<i>Dicentra spectabilis</i>	.	.
	<i>Matthiola incana</i> , var. <i>bicornis</i>	.	.
	<i>Barbarea vulgaris</i>	+	+
	<i>Nasturtium officinale</i>	+	.
	* <i>Cardamine pratensis</i>	+	+
	<i>Sisymbrium officinale</i>	+	.
	<i>S. albiaria</i>	+	.
	<i>Alyssum saxatile</i>	+	.
	<i>Iberis sempervirens</i>	+	.
	<i>Capsella bursa-pastoris</i>	.	.
	<i>Aubrietia deltoidea</i>	+	+
Violaceae	<i>Lunaria annua</i>	+	+
	<i>Viola riviniana</i>	.	.
	<i>V. arvensis</i> agg.	.	.
	<i>Viola</i> (cultivated)	+	.
Polygalaceae	<i>Polygala vulgaris</i>	+	.
Caryophyllaceae	<i>Dianthus barbatus</i>	+	.
	<i>Saponaria officinalis</i>	+	.
	<i>Lychnis alba</i> , S	.	.
	<i>L. dioica</i> , S	+	.
	* <i>L. flos-cuculi</i>	+	+
	<i>L. coronaria</i>	.	.
	<i>Arenaria montana</i>	.	.
	<i>Cerastium vulgatum</i>	+	.
	<i>C. tomentosum</i>	.	.
	<i>Stellaria graminea</i>	+	+
	<i>S. holostea</i>	+	+
Aizoaceae	* <i>Spergula arvensis</i> , S	+	.
	<i>Mesembryanthemum crystallinum</i>	+	.
	<i>Tamarix gallica</i>	+	+
	<i>Linum catharticum</i>	+	.
	<i>Malva</i> sp.	+	+
	<i>Geranium sanguineum</i>	+	.
	<i>G. pratense</i>	+	+
	<i>G. robertianum</i> , S	.	.
	<i>G. dissectum</i> , S	.	.
	<i>Pelargonium peltatum</i>	+	+
	<i>Tropaeolum majus</i>	+	+
Oxalidaceae	<i>Oxalis acetosella</i> , S	.	.
	<i>O. purpurea</i>	.	.
	* <i>Acer campestre</i>	+	+
Aceraceae	<i>A. pseudo-platanus</i>	+	+
	<i>Euonymus europaeus</i>	.	.
Celastraceae	<i>Rhamnus frangula</i>	+	+
Vitaceae	<i>Vitis</i> (cultivated)	+	.
Anacardiaceae	<i>Rhus cotinus</i>	+	.
Leguminosae	<i>Ulex europaeus</i>	+	+
	<i>Genista anglica</i>	+	+

Table 4 (continued)

Family	Species	Known to receive visits from honey bee	Pollen collection observed
Leguminosae (continued)	<i>Medicago lupulina</i>	+	.
	<i>Trifolium procumbens</i>	+	.
	<i>Lotus uliginosus</i>	+	.
	<i>Vicia cracca</i>	+	.
	<i>V. hirsuta</i> , S	.	.
	<i>V. sepium</i>	+	.
	<i>V. angustifolia</i>	.	.
	<i>Lathyrus odoratus</i>	+	.
	<i>L. pratensis</i>	.	.
	<i>L. tuberosus</i>	.	.
	* <i>Spartium junceum</i>	.	.
	<i>Pisum sativum</i>	.	.
	<i>Robinia pseudo-acacia</i>	+	.
	<i>Cytisus laburnum</i>	+	.
	<i>Lupinus polyphyllus</i>	+	+
	<i>Wistaria floribunda</i>	+	+
Rosaceae	<i>Prunus cerasus</i>	+	+
	<i>Spiraea arguta</i> , S	.	.
	<i>Geum urbanum</i>	.	.
	<i>G. rivale</i>	+	.
	<i>Fragaria</i> (cultivated)	+	+
	<i>Potentilla reptans</i>	.	.
	* <i>P. erecta</i>	.	.
	* <i>P. palustris</i>	.	.
	<i>Rosa canina</i>	+	+
	<i>R. arvensis</i>	+	+
	<i>R. spinosissima</i>	+	+
	<i>Pyrus communis</i>	+	+
	* <i>P. malus</i>	+	+
	<i>Cotoneaster horizontalis</i> , S	+	+
	<i>Kerria japonica</i>	.	.
Onagraceae	<i>Epilobium montanum</i>	+	.
	<i>E. hirsutum</i>	+	.
	<i>Circaea lutetiana</i>	.	.
	<i>Clarkia</i> sp.	.	.
Crassulaceae	<i>Fuchsia magellanica</i>	+	.
Ribesaceae	<i>Sedum acre</i>	+	.
	<i>Ribes sanguineum</i>	+	+
	<i>R. nigrum</i>	+	.
Escalloniaceae	<i>Escallonia</i> sp., S	+	.
Hydrangeaceae	<i>Hydrangea opuloides</i>	+	.
	* <i>Philadelphus coronarius</i>	+	+
Saxifragaceae	<i>Saxifraga stracheyi</i>	+	.
	<i>S. umbrosa</i>	+	.
	<i>Heuchera sanguinea</i>	+	.
Rutaceae	<i>Choisya ternata</i>	.	.
Umbelliferae	<i>Sanicula europaea</i>	.	.
	<i>Apium graveolens</i>	+	.
	* <i>Oenanthe crocata</i>	.	.
	<i>Angelica sylvestris</i>	.	.
	<i>Pastinaca sativa</i>	+	.
	<i>Anthriscus sylvestris</i>	+	+
	<i>Petroselinum sativum</i>	+	.
	<i>Aucuba japonica</i> , S	.	.
	<i>Viburnum opulus</i>	+	+
	<i>V. tinus</i>	+	+
Cornaceae	<i>Lonicera periclymenum</i>	+	+
Caprifoliaceae	<i>Symphoricarpos racemosus</i>	+	+
	<i>Syringa vulgaris</i>	+	+
Oleaceae	<i>Galium aparine</i>	.	.
Rubiaceae	<i>G. uliginosum</i>	.	.
Dipsacaceae	* <i>Scabiosa succisa</i>	+	.
	<i>S. arvensis</i>	+	+

Table 4 (continued)

Family	Species	Known to receive visits from honey bee	Pollen collection observed
Compositae	<i>Erigeron</i> sp.	+	.
	<i>Solidago canadensis</i>	+	+
	<i>S. virgaurea</i>	+	+
	* <i>Bellis perennis</i> , S	+	+
	<i>Chrysanthemum leucanthemum</i>	+	.
	<i>Matricaria chamomilla</i>	+	+
	<i>Anthemis</i> sp.	.	.
	<i>Achillea millefolium</i>	+	+
	<i>Senecio vulgaris</i>	+	.
	<i>S. jacobaea</i>	+	+
	<i>Doronicum plantagineum</i>	+	+
	<i>Arctium lappa</i>	+	+
	<i>Centaurea cyanus</i>	+	+
	<i>C. moschata</i>	+	+
	<i>Tragopogon pratensis</i>	.	.
	* <i>Leontodon hispidus</i>	+	+
	<i>Lactuca muralis</i> , S	.	+
	<i>Sonchus arvensis</i>	+	+
	<i>S. oleraceus</i>	+	+
	* <i>Crepis taraxacifolia</i>	+	+
	* <i>Hieracium murorum</i>	.	.
	<i>H. pilosella</i>	+	.
	<i>H. aurantiacum</i>	+	+
	<i>Dahlia</i>	.	.
	<i>Matricaria suaveolens</i>	.	+
	<i>Echinops</i> sp.	+	+
	<i>Cirsium lanceolatum</i>	.	(probable)
	<i>Helenium autumnale</i>	+	+
	<i>Helichrysum bracteatum</i>	+	+
	<i>Calendula officinalis</i>	+	.
	<i>Pyrethrum roseum</i>	.	.
Lobeliaceae	<i>Lobelia erinus</i>	.	.
Campanulaceae	<i>Campanula pyramidalis</i>	+	+
	<i>C. rotundifolia</i>	+	+
Primulaceae	<i>C. media</i>	+	+
	<i>Primula elatior</i> (Polyanthus), S	+	.
	<i>Lysimachia nemorum</i> , S	.	.
Plumbaginaceae	<i>L. vulgaris</i>	+	+
	<i>L. nummularia</i>	.	.
	<i>Anagallis arvensis</i>	.	.
Gentianaceae	<i>Armeria vulgaris</i>	.	.
Polemoniaceae	<i>Centaureum umbellatum</i>	.	.
	<i>Phlox subulata</i>	.	.
Convolvulaceae	<i>P. paniculata</i> , S	.	.
	<i>Convolvulus arvensis</i>	+	+
Boraginaceae	<i>Myosotis sylvatica</i> , S	+	+
	<i>Anchusa italica</i>	+	.
Solanaceae	<i>Symphytum officinale</i>	+	+
	<i>Solanum dulcamara</i>	+	+
	* <i>S. lycopersicum</i> , S	+	+
Scrophulariaceae	<i>Nicotiana glauca</i>	+	.
	<i>Verbascum thapsus</i>	+	+
	<i>Antirrhinum majus</i>	+	+
	<i>Linaria vulgaris</i>	+	.
	<i>L. cymbalaria</i>	.	.
	<i>Pentstemon gloxinoides</i>	+	.
	<i>Scrophularia nodosa</i>	+	+
	<i>Veronica chamaedrys</i> , S	+	+
	<i>V. buxbaumii</i> , S	.	.
	<i>V. speciosa</i>	+	.
	* <i>Rhinanthus crista-galli</i>	+	.

Table 4 (continued)

Family	Species	Known to receive visits from honey bee	Pollen collection observed
Scrophulariaceae (continued)	<i>Euphrasia officinalis</i>	+	.
Labiatae	* <i>Pedicularis sylvatica</i> , S	.	.
	<i>Lycopus europaeus</i>	+	.
	<i>Thymus serpyllum</i>	+	.
	<i>Nepeta hederacea</i> , S	+	+
	<i>N. marifolia</i>	+	.
	<i>Prunella vulgaris</i>	+	.
	<i>Stachys betonica</i>	+	.
	<i>S. officinalis</i> , S	+	.
	<i>Lamium galeobdolon</i> , S	+	.
	<i>Ajuga reptans</i>	+	+
	<i>Rosmarinus officinalis</i>	+	.
	<i>Scutellaria galericulata</i>	.	.
	<i>Lavandula vera</i> , S	+	.
Cucurbitaceae	<i>Cucurbita pepo</i> (vegetable marrow)	+	+
	<i>Cucumis sativus</i>	+	+
Polygonaceae	* <i>Rumex acetosa</i>	.	.
	<i>Polygonum hydropiper</i>	.	.
Euphorbiaceae	<i>Euphorbia amygdaloides</i> , S	+	.
	<i>E. helioscopia</i> , S	+	.
Urticaceae	<i>Urtica dioica</i>	+	.
Fagaceae	* <i>Fagus sylvatica</i>	+	+
Araceae	<i>Arum maculatum</i>	.	.
	<i>Richardia africana</i>	.	.
Orchidaceae	<i>Orchis maculata</i>	+	.
Iridaceae	<i>Iris pseudacorus</i>	+	.
	<i>I. germanica</i>	.	.
Dioscoridaceae	<i>Tamus communis</i>	+	.
Lilaceae	<i>Polygonatum multiflorum</i>	+	.
	<i>Convallaria majalis</i>	+	+
	<i>Tulip gesneriana</i> (Darwin T.)	+	+
	<i>Kniphofia uvaria</i>	+	.
	<i>Hemerocallis flava</i>	.	.
	<i>H. fulva</i>	.	.
	<i>Muscari botryoides</i>	+	+
	<i>Yucca gloriosa</i>	.	.
	<i>Allium schoenoprasum</i>	+	+
Pinaceae	* <i>Pinus montezumae</i>	.	.
	* <i>P. sylvestris</i>	+	+

In Table 5 the 'attractive' qualities of these relatively abundant yet unvisited species are analysed in terms of food for the bees. The availability and relative abundance of nectar are based on observations in previous years. The relative abundance of pollen is assessed not per flower but per *flower form*: for example, a composite inflorescence is considered to be a single unit, as it is this latter unit which is probably the significant one for the bee. If it was found that insufficient pollen to make a pollen slide was gathered from such a unit, the pollen was deemed to be 'scanty'. The role of scent in the biological relationship between flower and honey bee has been explained by Von Frisch; and the presence of scent has been noted in a fourth column for general interest.

We see from the analysis that each species, except only *Crepis taraxacifolia*, lacks, or is relatively deficient in, one bee food as compared with the relatively abundant visited species. (The case of *C. taraxacifolia* is unexplained. It has an attractive complement equal to that of the visited species. It may have been too far away, the first concentration of plants being only just within the $\frac{1}{4}$ -mile radius and situated in a hollow, separated by

rising ground, north-west from the hives.) These species then, although the lack or paucity of one bee food does not prevent bees visiting them in other floral combinations, are, in this neighbourhood, handicapped by their poorer attractive complement. This discounts the fact that they are relatively abundant. *The bees in this area foraged the abundant species which offered nectar and (or) pollen in quantity per flower form.*

Table 5. *Analysis of attractive complement in terms of food for bees of species forming stands from which no pollen was collected*

Species	Pollen	Nectar	Scent
<i>Bellis perennis</i>	Scanty	Available but scanty	Present
<i>Crepis taraxacifolia</i>	Rel. abundant	Rel. abundant	Present
<i>Hieracium murorum</i>	Scanty	Rel. abundant	Present
<i>Rhinanthus crista-galli</i>	Scanty	Not available to honey bee	Present
<i>Rumex acetosa</i>	Rel. abundant	None	None
<i>Fagus sylvatica</i>	Rel. abundant	None	None
<i>Philadelphus coronarius</i>	Rel. abundant	Very scanty	Present
<i>Solanum lycopersicon</i>	Scanty	None	None
<i>Vitis vinifera</i>	Scanty	Present	Present
<i>Pinus sylvestris</i>	Abundant	None	None
<i>P. montezumae</i>	Abundant	None	None

DURATION OF FLOWERING OF SPECIES AND THE PERIODS WITHIN WHICH
THEY WERE WORKED FOR POLLEN BY THE HONEY BEE

In Table 3 the dates of the flowering of the species from which the bees collected pollen are given together with the period for which the bees exploited them. These dates nearly coincided in a majority of cases, that is the plants were worked from first blooming to the end of the flowering period. There are exceptions; the more pronounced discrepancies in dates are marked with an asterisk in Table 3, col. 3. On examination of the floral notes it is found that these can be largely discounted. The discrepancy appears either at the beginning or end of the flowering period. *Cirsium arvense*, *C. palustre*, *Teucrium scorodonia*, *Ulex gallii*, *Diervilla japonica*, *Aconitum napellus*, *Campanula*, *Oenothera biennis*, *Clematis vitalba*, *Rubus fruticosus*, *Alisma plantago-aquatica*, *Ligustrum vulgare*, *Lotus corniculatus* and *Papaver orientale* appear to be in flower from 10 days to 7 weeks before exploitation by the bees. The first nine of these species were represented only by single plants or a few individuals growing more than $\frac{1}{4}$ mile away and were in the built-up area of Radyr village. *Alisma*, *Ligustrum*, *Lotus* and *Papaver* and an early flowering species included in *Rubus fruticosus* agg. were within 300 yd. of the hive but were represented by virtually single flowers. As soon as any of these species bloomed in any quantity near the hives they were worked for pollen. The abandonment of a crop by the bees appreciably before flowering was over was less common. *Vicia faba*, *Sambucus nigra* and *Ranunculus bulbosus* ceased to be visited as soon as there was any quantity of *Trifolium repens* and *Rubus fruticosus*. There was but little bloom left on the beans and elder, but the buttercup was still fairly abundant. The period of flowering of *Sarothamnus scoparius* was lengthened by the late blooming of two bushes just outside the $\frac{1}{2}$ -mile limit. The bees only worked the near flowering bushes north of the hives, as the records cease when these finished flowering. Sometimes pollen collection from a species in almost continuous flower was spasmodic. It was only when individuals near the hive were in flower that their pollen was recorded. This is the case for *Aconitum napellus*, *Chieranthus cheiri*, *Taraxacum*

officinale and *Polygonum persicaria*. *Kentranthus ruber* and *Rubus loganobaccus* (loganberry) which were within 25 yd. of the hive and in sunny positions, were often exploited before recording began in the morning.

The case of *Trifolium pratense* deserves notice. A constant watch was kept for the pollens of *Trifolium pratense* and *Lotus corniculatus*, as they are similar in colour to that of *Trifolium repens*. Of 401 pollen balls adjudged 'white clover brown' examined throughout the season, three were *Lotus*, one was *Trifolium pratense*, one *Cornus sanguinea*, one *Phaseolus multiflorus* and one a six-furrowed grain of an unidentified Labiate. The rest were all *Trifolium repens* pollen. Only this single load of *T. pratense* was found and that at 5 p.m. on 26 June. It was reckoned on a percentage basis of the number of white clover loads for the 5-5.35 p.m. period that possibly sixty-six of these were *T. pratense*. Reckoned as a percentage of the whole season's income the total figure for *T. pratense* is 338. Whichever figure is taken it is seen that red clover is very little worked for pollen in this area. The red clover is only sparsely distributed in the hay fields and pastures.

Hypochaeris radicata was the longest-flowering crop being continually in bloom from 16 May to 23 August. It was exploited for pollen for the whole of this period, the great bulk being collected from 31 May to 24 June, i.e. before the hay was cut. Only small amounts were gathered subsequently from pastures and aftermaths.

There were two crops of *Sinapis arvensis*, whose flowering barely overlapped. From 5-28 July the bees did not work it for pollen, undoubtedly because: (a) there were very few blooms open; (b) the flowering of white clover and blackberry was at its height; (c) because the late crop of charlock was in a field beyond two of the clover fields. It was strongly worked as soon as the clover and blackberry diminished.

TIME OF DAY AT WHICH POLLEN FROM DIFFERENT SPECIES WAS GATHERED
(Table 3, col. 5)

Variation in the species composition of the pollen income throughout the day was a marked feature of the daily returns. The three main Rosaceous sources, *Rubus fruticosus*, *R. idaeus* and *Crataegus monogyna*, were exploited all day. The apparent lag of an hour in the morning in the *Crataegus* record is not actual, as the bees were not active before 9 a.m. in the spring. *Trifolium repens* was not exploited for pollen for nearly an hour after *Rubus fruticosus* during the nectar flow. Of the other two main Leguminous sources, *Sarothamnus scoparius* and *Vicia faba*, the former was worked chiefly in the morning, the latter in the afternoon. *Cornus sanguinea*, *Heracleum sphondylium* and *Castanea sativa* were 'morning crops' and were the first pollens to be brought in each morning together with a few loads of *Papaver orientale*, *Hypericum* sp., *Helianthemum chamaecistus*, *Phaseolus multiflorus*, *Aconitum napellus* and *Clematis vitalba*. *Hypochaeris radicata* was another morning crop but was always exploited an hour later than the species just mentioned. *Alisma plantago* pollen was recorded only between 11 a.m. and 1.30 p.m. The pollen of the species named above was brought in steadily throughout the whole of the periods stated for collection. This was also true of collection from many minor sources and from the Rust fungus. Sudden and short-lived periods of collection were observed on several occasions; the most striking being that of 298 loads of *Polygonum persicaria* between 1 and 2 p.m. on 12 August. One bee alone worked *Scilla non-scripta* bringing in its blue loads regularly on each $\frac{1}{2}$ -hour of the day.

One clear poof of the changing over of bees from one crop to another was obtained. It happened in the spring that the bees worked *Sarothamnus* in the morning and *Crataegus* later in the day. The same bees were involved for they still had their thoraces daubed between the wings with orange *Sarothamnus* pollen while bearing in their corbiculae the pale yellow-green balls of *Crataegus* pollen.

Taken in conjunction with the floral and weather data these results can to some extent be explained. The all-day collection from *Rubus fruticosus*, *R. idaeus*, *Crataegus monogyna* and *Trifolium repens* seems to be due to the fact that there is an abundant supply of these pollens which is not exhausted during the day as compared with the smaller crops of *Alisma plantago-aquatica*, *Cornus sanguinea*, etc. *Rubus fruticosus* is known to secrete nectar all day (Percival, 1946); and this probably is another factor in holding the bees to the crop even if their object is primarily pollen collection.

The early morning pollens all come from plants *near the hive and growing in spots on which the morning sun first strikes*. These plants have pollen available because the warmth of the sun desiccates the anthers and the flowers have dry petals. This latter fact seems to be significant, for bees do not collect pollen if the petals are dewy. The lag of 1 hr. before morning collection of *Trifolium* pollen is explained on these grounds. The pastures take about 1 hr. longer to dry compared with the hedgerows. Thus early exploitation of these species is due to close proximity to the hive and the sunny position in which the plants grow.

The time of collection from *Hypochaeris radicata* coincides with the period of maximum extension of the capitulum but further data are required on the pollen presentation of the florets before the cessation of collection in the afternoon can be explained. It has been stated that honey bees do not exploit *Hypochaeris* for nectar, so this may be a case of competition between *Trifolium repens* and *Hypochaeris*—the former winning over the bees in the afternoon—a parallel to the *Sarothamnus*-*Crataegus* change-over in the spring. This also may be due to the fact that *Crataegus* provides nectar as well as pollen. The first question to be answered however is: Why is *Sarothamnus* worked in the morning? Perhaps fresh pollen is needed in the hive in quantity in the morning and *Sarothamnus* (and *Hypochaeris*) could supply this abundantly. The observer had a strong impression that in the early morning, a far greater percentage of the foraging bees returned with pollen than later in the day, but this is not supported by actual counts.

The most clear-cut and limited period of pollen collection from any species was that of *Alisma plantago-aquatica*. The flowers, which live only one day, have their petals unfolded but erect at 10 a.m. and are not fully open until half an hour later. Pollen is presented at 10.45 a.m. and loads are recorded during the 11–11.35 a.m. period until 1.35 p.m. The flowers remain open for the rest of the day, so presumably pollen collection ceases owing to exhaustion of supply; for the bees were seen to work the flowers until after 4 p.m. There was only one stand of the plant growing on the fringe of a pond 150 yd. from the hive, so the supply available was restricted.

The afternoon collection of pollen from *Vicia faba* may be explained by the distance of the crop from the hive. The bean fields were $\frac{1}{3}$ mile away and 145 ft. below the level of the hive. There was also a strong resident population of eleven stocks of bees beside the bean fields. It is thought that bees work the nearest crops first and forage further afield later in the day. This seems to be confirmed by the case in point.

The source of the rust spores which were collected 3–18 August was not traced. The spores most nearly resembled the uredospores of *Coleosporium senecionis*.

WEATHER CONDITIONS AND POLLEN COLLECTION

Sun and Cloud. The effect of weather conditions on the collection of pollen is primarily an effect of the weather on the activity of the flying bees as a whole. In warm, calm weather, whether sunny or not, the bees foraged most freely and the pollen income was also large. Sunny days, however, did accelerate both the opening of the flowers and the foraging activity; and bursts of flowering coincided with peaks in pollen income.

The bees were very sensitive to changes in light intensity. The approach of a heavy cloud bank sent the foragers home. Bees working in open fields on clover returned immediately; those working among blackberry bushes did not return so precipitously. This is noticeable in the pollen-load counting. For the first minute or so of the 'return home' period, most of the bees are those carrying the brown loads of *Trifolium repens* pollen. After the second minute most of the clover bees are in, and a preponderance of bees with grey loads of pollen from the blackberry are returning. As these two crops were well distributed in the area the factor of distance is eliminated. The explanation seems to be that the bees working the hedgerows do not become aware of the impending change as soon as those working in the open fields.

Table 6. *No. of pollen loads recorded*

	14 July	16 July	17 July
<i>Trifolium repens</i>	3764	521	4191
<i>Rubus fruticosus</i>	3716	2701	3938
<i>Teucrium scorodonia</i>	—	461	35

Rain. One condition, rain, absolutely stops pollen collection. Even slight rain is effective in doing this, although the bees continue to forage for nectar in drizzling rain. The reason seems to be the mechanical difficulty of successful transference of the pollen to the pollen basket. Although the anthers close in flowers in which the stamens are exposed, pollen is available and dry in the legumes (*Sarothamnus*, *Trifolium* and *Vicia*), yet none is collected.

Pollen collection restarts very quickly after rain. Within 30 min. of cessation pollen was brought into the hive. This came from all the species being worked. There was no indication that 'protected' pollen was brought in preferentially or any sooner than that from 'open' flowers, but on 3 July, a day of intermittent rain, a much greater amount of white clover pollen was brought in compared with the amount of blackberry (Fig. 3).

Wind. The effect of wind is on the general activity of the foragers. Strong winds (1200–2500 ft./min.), accompanied by low temperatures cut down foraging and therefore diminish pollen collection. Air movement below 1000 ft./min. has no observable effect.

Wind direction influences the direction in which the bees forage if the wind is sufficiently strong. This was seen on 16 July when the air movement averaged 2100 ft./min. from the west. The amount of *Trifolium repens* pollen was sharply reduced, *Rubus fruticosus* maintained a fairly high level, and 461 loads of *Teucrium scorodonia* pollen were recorded (Table 6). The *Teucrium* was growing on a sheltered roadside bank where the road drops sharply to the east of the hive and the seven acres of blackberry to the north were also on ground sloping eastwards. On the following day, with the wind south-south-east at an average rate of 700 ft./min., clover was abundantly worked while only

thirty-five loads of *Teucrium* came in. The clover fields were west of the hive and fully exposed to the wind. Bees, therefore, do not forage in exposed pastures in the teeth of the wind.

In Fig. 3 the pollen income from the two major crops, *Trifolium repens* and *Rubus fruticosus*, is shown graphically together with the meteorological data. This confirms the general preceding remarks on the influence of the weather conditions on pollen income. Some apparent anomalies can be explained. For instance, on 10-11 July there was a marked diminution in the *Trifolium repens* pollen income which cannot be accounted for on the grounds of unequable weather. On these dates 27 acres of hay were cut (see flower map 10-14 July, Fig. 15) within the foraging area. Moreover both white clover and blackberry were approaching the end of their main peak of flowering. Blackberry had a second flowering peak from 23 July to 2 August, but the clover steadily diminished; and this is reflected in the relatively smaller yields of pollen from the latter during this period. The effect of a sunless day after a sunny one is usually a strong depression in pollen income, and is chiefly due to less foraging activity.

The amount of blackberry pollen 'presented' varies considerably from day to day. Examination of some hundreds of flowers in different positions at noon on 8 July, 10 a.m. on the 9th and 9.30 a.m. on the 14th, showed virtually no available pollen and accounts for the smaller income from blackberry on these dates. The variation has its foundation in the fact that the blackberry's flowers open in groups, separated by one or two days' lull (Percival, 1946). This alone would give a varying supply of pollen, but it can be aggravated by the weather in that a sunny day will bring a great many flowers to the conclusion of the male phase; and this cannot be repeated for a day or so until the next batch of flowers is ready to open.

That such events as intermittent pollen presentation in the blackberry and the cutting of hay are reflected in the pollen income, indicate that the neighbourhood must be practically 'saturated' by the hive-bee population.

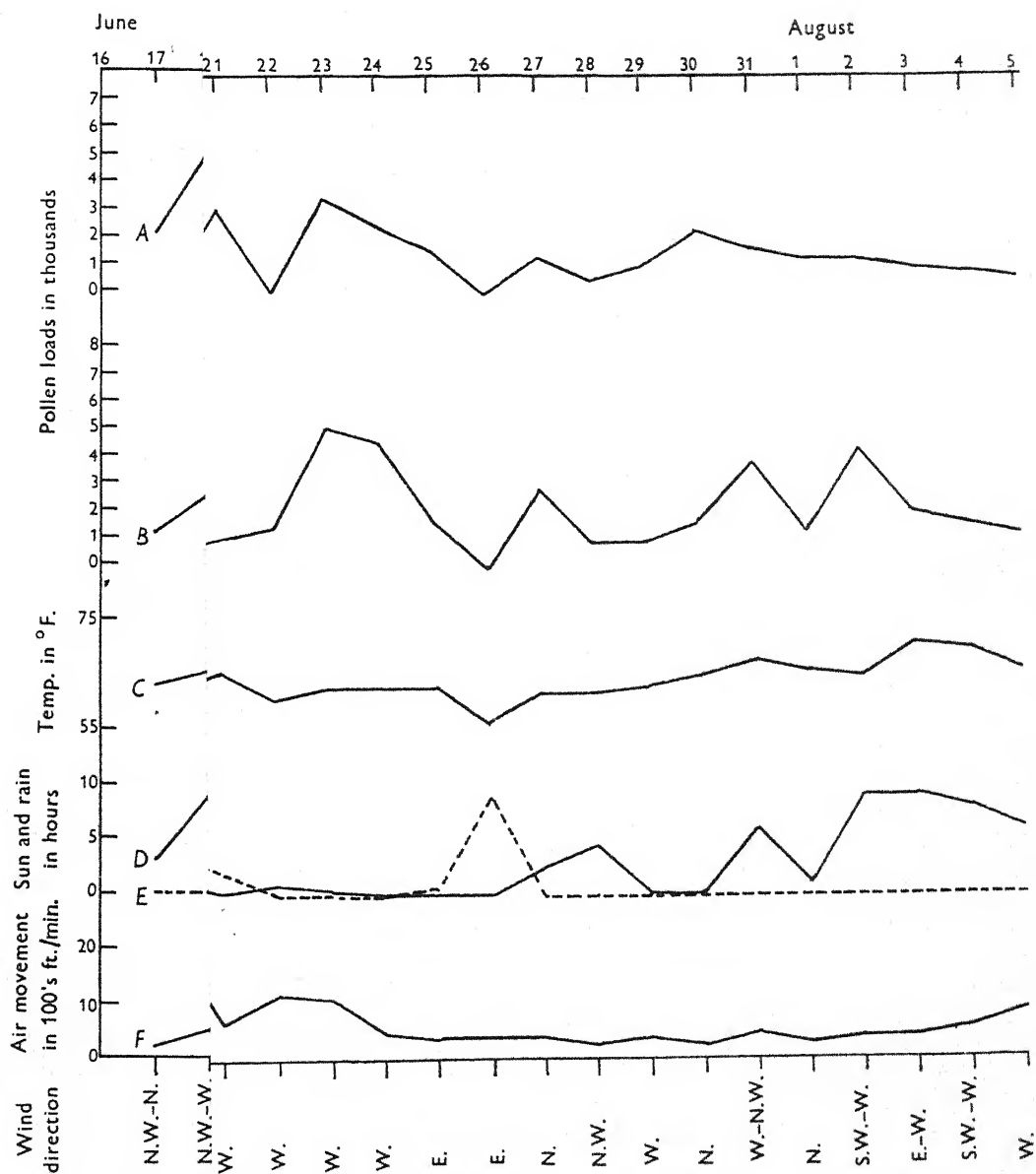
MIXED LOADS OF POLLEN

The conservative traits of the honey bee while foraging which has been observed by other workers, receives additional confirmation from the pollen records, in that the number of loads of mixed pollen recorded is very small. A total of 256 mixed loads was recorded, representing but one-thousandth of the total pollen incomes. An analysis of these is seen in Table 7.

All were two-species mixtures except three which were three-species mixtures. I failed to identify one or both components in fifteen loads.

Hypochaeris radicata and *Trifolium repens* mixtures were by far the most common, exceeding by four times in number those of *Epilobium angustifolium* and *Rubus fruticosus*. These species were all major pollen sources.

On examination of the species list, together with the floral maps, it was seen that in all cases the mixtures were obtained from plants which were contiguous. Not only were the plants growing together, but in most cases they bore flowers at the same height so that both a lateral and vertical proximity obtained. These two seem to be the only significant factors in interpreting the gathering of mixed loads by the bee. The flowers selected have nothing else in common, being widely different in size, colour, scent and structure.



average day temperature; D=sunshine; E=rain; F=air movement.

Table 7. *Mixed loads of pollen*

Names of species	No. of loads recorded	Arrangement of pollen in loads
<i>Sarothamnus scoparius</i> + <i>Crataegus monogyna</i>	1	Intermingled
<i>S. scoparius</i> + <i>Cornus sanguinea</i>	1	Two blocks
<i>S. scoparius</i> + <i>Vicia faba</i>	1	Two blocks
<i>Crataegus monogyna</i> + <i>Ilex aquifolium</i>	1	Intermingled
<i>Taraxacum officinale</i> + <i>Helianthemum chamaecistus</i>	1	Intermingled
<i>Rubus idaeus</i> + <i>R. fruticosus</i>	1	Intermingled
<i>Hypochaeris radicata</i> + <i>Brassica arvensis</i>	3	Two blocks
<i>Lotus corniculatus</i> + <i>Trifolium repens</i>	4	Intermingled
<i>Ranunculus bulbosus</i> + <i>R. acris</i>	1	Intermingled
<i>Cornus sanguinea</i> + <i>Brassica arvensis</i>	1	Intermingled
<i>Hypochaeris radicata</i> + <i>Sambucus nigra</i>	1	Intermingled
<i>Vicia faba</i> + <i>Ranunculus bulbosus</i>	1	Intermingled
<i>Helianthemum chamaecistus</i> + <i>Kentranthus ruber</i>	2	Two blocks
<i>Trifolium repens</i> + <i>Ranunculus bulbosus</i>	1	Intermingled
<i>T. repens</i> + <i>Plantago lanceolata</i>	1	Intermingled
<i>Tilia europaea</i> + <i>Castanea sativa</i>	1	Intermingled
<i>Hypochaeris radicata</i> + <i>Trifolium repens</i>	132	131 in two blocks; 1 intermingled
<i>H. radicata</i> + <i>Aegopodium podagraria</i>	1	Intermingled
<i>Tilia europaea</i> + <i>Helianthemum chamaecistus</i>	1	Two blocks
<i>Epilobium angustifolium</i> + <i>Epilobium</i> sp.	1	Two blocks
<i>Ligustrum vulgare</i> + <i>Buddleia variabilis</i>	1	Intermingled
<i>Hypochaeris radicata</i> + <i>Lotus corniculatus</i>	5	Intermingled
<i>Cirsium arvense</i> + <i>Raphanus raphanistrum</i>	8	Intermingled
<i>Hypochaeris radicata</i> + <i>R. raphanistrum</i>	18	Two blocks
<i>Epilobium angustifolium</i> + <i>Rubus fruticosus</i>	36	35 intermingled; 1 in two blocks
<i>Heracleum sphondylium</i> + <i>Clematis vitalba</i>	1	Two blocks
<i>H. sphondylium</i> + <i>Ranunculus acris</i>	1	Intermingled
<i>Trifolium repens</i> + <i>Centaurea nigra</i>	1	Intermingled
<i>Plantago lanceolata</i> + <i>Mentha</i> sp.	1	Two blocks
<i>Alisma plantago-aquatica</i> + <i>Sparganium erectum</i>	8	7 intermingled; 1 in three blocks
<i>Sinapis arvensis</i> + <i>Raphanus raphanistrum</i>	1	Intermingled
Unidentified in one component	15	
<i>Centaurea nigra</i> + <i>Teucrium scorodonia</i>	1	Three blocks
<i>Sarothamnus scoparius</i> + <i>Taraxacum officinale</i> + <i>Ranunculus bulbosus</i>	2	Intermingled
<i>Helianthemum chamaecistus</i> + <i>Campanula</i> sp + Unidentified.	1	Two layers

MODE OF COLLECTION

Three different arrangements of the pollens in the loads were noted.

The pollens were: (a) intermingled; (b) in two distinct blocks; (c) in three distinct blocks.

The *Rubus fruticosus*-*Epilobium angustifolium* loads were intermingled giving a load of a distinct saxe-blue shade. The *Hypochaeris radicata*-*Trifolium repens* loads were nearly always in two blocks, orange and brown respectively. Sometimes the clover was gathered first, sometimes the *Hypochaeris*. Why there should be this difference in the method of collecting from these two pairs of species is not known. From the point of view of effective cross-pollination, the two-block method of collection has limitations, compared with the intermingling method. The latter indicates frequent cross-collection between the two species concerned, the former but one. It has no practical biological significance in these particular cases as the plants are unrelated. Very occasionally a sandwich arrangement of the pollen was seen. A grey-pink-grey load proved to be *Centaurea nigra*, *Teucrium scorodonia* and *Centaurea nigra*. A pale yellow, dark yellow, pale yellow load was a block of *Alisma plantago* between two blocks of *Sparganium erectum* pollen. Of the three-species mixtures, two were 'intermingled' loads of *Sarothamnus scoparius*, *Taraxacum*

officinale and *Ranunculus bulbosus*; one, an orange load edged with brown, was chiefly *Helianthemum chamaecistus* with a little *Campanula* and an unidentified pollen as an edging.

It will be seen from an examination of Table 7 that the chance of interspecific crosses being effected by honey bees is very slight in the neighbourhood of Radyr. The first reason for this is the conservative foraging habit of the honey bee. The second is the position of the crops; for if lateral and vertical proximity are necessary for even the rare cross-collection of pollen, closely related species must grow together if they are to be crossed. This occurs but seldom in this district, but where it does occur the 'proximity' factor has a significance. Three interspecific crosses might have been effected, namely, *Ranunculus bulbosus* \times *R. acris* and *Epilobium angustifolium* \times *Epilobium* sp. and *Rubus fruticosus* \times *R. idaeus*. The product of the last pair, the loganberry, has been found in the 7-acre blackberry-raspberry patch. A big stand of *E. angustifolium* also occurs in this same patch, which was a beech wood until the spring of 1940. A small stand of *E. tetragonum* is contiguous with *E. angustifolium* at one point, and the unidentified pollen probably is that of *E. tetragonum*. *E. angustifolium* is known to be a very stable species but a type which may have been of hybrid origin appeared in the patch in 1944. Unfortunately the plant has not been seen since.

A group among which cross-pollination must be very frequently effected by the bees is that of the blackberries. At least seven types, believed to be distinct and of species rank, occur within 100 yd. of the hive. The crop is heavily worked by the bees both for nectar and pollen; but whether hybrids exist or if they result from the honey bees' activities, is not known.

The independent collection of *Sinapis arvensis* and *Raphanus raphanistrum* pollen is worthy of notice. The second crop charlock and the radish were growing together in the same root crop. They were in flower at the same time, yet only one mixed load was recorded from these two species. This is an example of the delicacy and precision of the relationship between insect and flower, depending in this instance on something less obvious than flower form and colour.

CHARACTERISTICS OF THE POLLEN LOADS

In Table 8 are shown certain of the characteristics of the pollen loads gathered from different species. The colours noted are as they appeared to the observer against a brown background. They were judged as the bee walked up the solignum-stained flight board. They refer, therefore, only to the tints of perfectly fresh loads of pollen.

It will be noted that the pollen from most species is packed into the corbiculae and the bee's body appears to be relatively immaculate. There are several notable exceptions in the Compositae (*Taraxacum*, *Hypochaeris* and *Cirsium*), and in the Brassicas, where the body is nearly always dusted when the bee returns.

When *Sarothamnus scoparius* has been visited, there is a thick patch of orange pollen on the thorax where the bee receives the blow from the recoiling style. The bees visiting *Impatiens roylei* are similarly marked with white and look somewhat ghost-like. The bees bear the thoracic patch of *Sarothamnus* pollen for hours after they have ceased to visit the broom, which they have worked in the morning, before changing over to visiting hawthorn in the afternoon. After visiting *Epilobium angustifolium* and *Teucrium scorodonia* the bees return with a patch of blue and chocolate pollen respectively on their foreheads. The viscous pollen of *Oenothera biennis* is partly gathered in the pollen baskets, but usually

Table 8. *Characteristics of pollen loads*

Species	Distribution of pollen on bee's body	Colour and texture of load
<i>Trifolium repens</i>	Corbiculae	Yellow-brown to dark brown
<i>Rubus fruticosus</i>	Corbiculae	Grey
<i>R. idaeus</i>	Corbiculae	Pale grey
<i>Crataegus monogyna</i>	Corbiculae	Greenish to pale yellow
<i>Sinapis arvensis</i>	Corbiculae and body dusted, patch on forehead	Pale apricot yellow, translucent
<i>Sarothamnus scoparius</i>	C., patch on thorax, general dusting of body	Bright orange
<i>Vicia faba</i>	Corbiculae	Blue-grey, granular
<i>Epilobium angustifolium</i>	C., patch on forehead	Peacock blue
<i>Raphanus raphanistrum</i>	C., body dusted	Greenish yellow
<i>Cornus sanguinea</i>	C.	Greenish to light yellow
<i>Heracleum sphondylium</i>	C.	Greenish yellow, opaque
<i>Castanea sativa</i>	C.	Lemon yellow
<i>Sambucus nigra</i>	C.	Sulphur yellow
<i>Centaurea nigra</i>	C. and body dusted	Pale pinkish grey
<i>Clematis vitalba</i>	C.	White to bluish white
<i>Ranunculus bulbosus</i>	C. and body dusted	Bright mid yellow
<i>Brassica oleracea</i> vars.	C.	Pale bright yellow
<i>Prunus lusitanica</i>	C.	Dirty white to pale biscuit
<i>Cirsium arvense</i>	C. and body dusted	Snow white, fluffy
<i>Teucrium scorodonia</i>	C. and patch on forehead	Chocolate, smooth
<i>Buddleia variabilis</i>	C.	White
<i>Alisma plantago-aquatica</i>	C.	Deep dull orange-yellow
Rust spores	C.	Vivid orange-red
<i>Plantago lanceolata</i>	C.	Very pale yellow, fluffy
<i>Helianthemum chamaecistus</i>	C.	Orange
<i>Sparganium ramosum</i>	C.	Lemon yellow
<i>Ligustrum vulgare</i>	C.	Lemon yellow
<i>Ulex gallii</i>	C.	Deep dull orange
<i>Impatiens roylei</i>	C., thorax heavily dusted	White
<i>Hypericum</i> spp.	C.	Orange
<i>Tilia europaea</i>	C.	Pale brown
<i>Polygonum persicaria</i>	C.	Dark grey
<i>Lotus corniculatus</i>	C.	Brown
<i>DierVilla japonica</i>	C.	Yellow
<i>Mentha</i> spp.	C.	White
<i>Filipendula ulmaria</i>	C.	Bright pale green
<i>Taraxacum officinale</i>	C. and body dusted	Bright yellow-orange
<i>Phaseolus multiflorus</i>	C.	Black
<i>Aconitum napellus</i>	C.	Black
<i>Papaver orientale</i>	C., whole body dusted	Deep purple
<i>Aegopodium podagraria</i>	C.	Grey
<i>Campanula</i> sp.	C.	Dirty white
<i>Aesculus hippocastanum</i>	C.	Red
<i>Ilex aquifolium</i>	C.	Pale yellow
<i>Oenothera biennis</i>	C. and trailing ribbons	Pale yellow
<i>Trifolium pratense</i>	C.	Brown
<i>Calystegia sepium</i>	C.	White
<i>Sorbus aucuparia</i>	C.	Greenish
<i>Montbretia pottsii</i>	C.	Glowing orange, translucent
<i>Cheiranthus cheiri</i>	C.	Greenish grey
<i>Eupatorium cannabinum</i>	C.	White
<i>Ranunculus acris</i>	C. and dusted	Bright yellow
<i>Scilla non-scripta</i>	C.	Blue
<i>Allium ursinum</i>	C.	Pale yellow
<i>Cirsium palustre</i>	C. and body dusted	Snowy white
<i>Salvia</i> sp.	C., patch on thorax	Yellow-white
<i>Digitalis purpurea</i>	C.	White
<i>Melilotus arvensis</i>	C.	Dull yellow
<i>Deutzia gracilis</i>	C.	Yellow
<i>Rhododendron ponticum</i>	C.	White
<i>Silene cucubalus</i>	C.	Dark brown
<i>Kentranthus ruber</i>	C.	Pale grey, fluffy
<i>Rubus loganobaccus</i>	C.	Greenish grey

trails from the basket as a ribbon, sometimes $\frac{1}{2}$ in. long. This pollen seems to be unmanageable within the hive, for the ribbons are often blown out of the hive by the hot draught along the floor board.

The significance of the distribution of the pollen on the bees' bodies in the floral biology of the particular plant species has not yet been investigated by the observer and cannot therefore be discussed.

CONCLUSION

A discussion of results and tentative explanations have been included in each of the foregoing sections. A consideration of these sectional results leads to the general conclusion that any plant offering a fair amount of pollen per flower-form, will be worked for pollen by the honey bee, provided that: (a) it grows within $\frac{1}{4}$ mile of the hive; (b) it attains a reasonable density.

The practical significance of this conclusion can only be determined by research into the intimate biological relationship between the honey bee and each species. It is obvious, however, that the composition of the flora and the position of the different crops in relation to the hive, have profound effects on the pollination potential of the different elements of the flora.

The author wishes to thank Metropolitan Vickers for the loan of the velometer, and also Miss D. Johns for her help in the preparation of the pollen samples, and the Radyr Girl Guides for their assistance in the floral survey.

SUMMARY

1. The pollen income of a colony of honey bees (*Apis mellifera*) was noted from 28 April to 23 August, 1945. The distribution, abundance and composition of the flora within a $\frac{1}{2}$ -mile radius of the hive were noted and meteorological data collected. An attempt was made to relate the data from these three sources, in order to gain some knowledge of the relationships between the honey bees and the flora.
2. The pollen income for the period was assessed at over a million loads; each load consists of two pollen balls.
3. Eighty-six different pollens were recorded. Sixty-six were identified.
4. A total of 256 loads of mixed pollen was recorded. The species from which these were collected seldom had floral features in common and were generally unrelated. The plants were contiguous and the flowers grew at the same height.
5. Pollen was chiefly collected from the major elements of the flora.
6. Peaks in pollen collection coincided with peaks in the flowering of the major species.
7. All pollen came from species which had individuals growing within the $\frac{1}{4}$ -mile radius of the hive. Those species whose nearest individuals grew outside this limit, even though they formed stands, were not worked for pollen.
8. The greatest amount of pollen came from the two main nectar sources, *Trifolium repens* and *Rubus fruticosus*.
9. Pollen collection depends to some extent on the amount of pollen available per flower form. The bees did not collect from flowers with scanty pollen.
10. Different species are worked for pollen at different times of day. This is explained

partly by proximity of crop; partly by times of presentation of pollen in the different species, and partly by competition between species.

11. Within the $\frac{1}{2}$ -mile area, 225 species with very sparse distribution were not worked for pollen.

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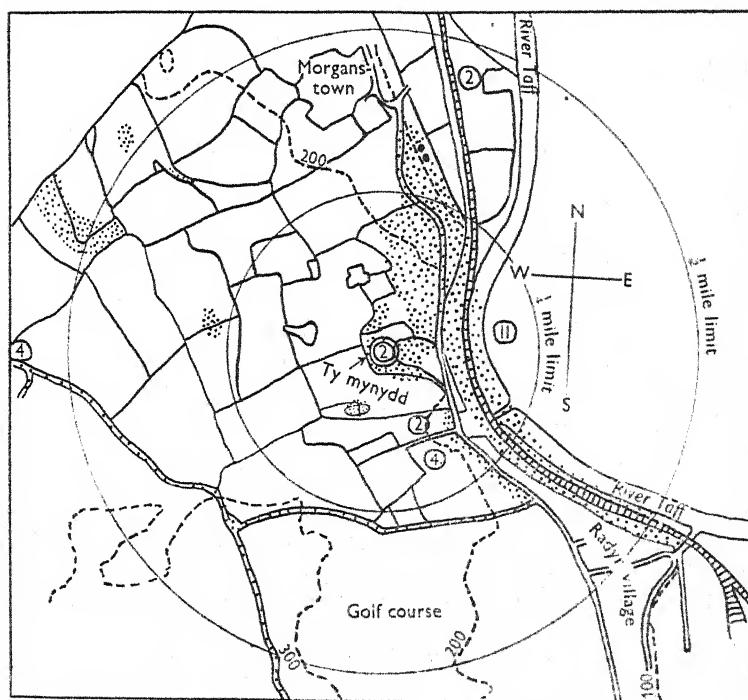


Fig. 4. Map of Ty Mynydd and district. ② = position of experimental hive. Position of other stocks of bees marked with a circle, and the number of stocks by the enclosed figure (e.g. ④). Stippled areas are those which are sheltered from the west wind.

Figs. 5-18. Maps showing the position of the major plants in the flora in bloom from April to August. The species are indicated by the letters (see key), the abundance of their blooms by the number of symbols within the enclosures:

- 1 symbol per enclosure=a few blooms only.
- 2 symbols per enclosure=blooms sparsely distributed (excepting the tree species).
- 3 symbols per enclosure=fair bloom.
- 4 symbols per enclosure=fairly abundant bloom.
- 5 and more symbols per enclosure=abundant bloom.
- Blackening-out of an enclosure indicates the cutting of the crop.

Fig. 5. April 24-27

Fig. 6. May 2-5

Fig. 7. May 10-11

Fig. 8. May 18

Fig. 9. May 25

Fig. 10. June 1

Fig. 11. June 12

Fig. 12. June 19

Fig. 13. June 25

Fig. 14. July 4

Fig. 15. July 10-14

Fig. 16. July 18

Fig. 17. July 27-Aug. 1

Fig. 18. Aug. 9-14

Key to species on flower maps

A, *Aesculus hippocastanum*; *Ap*, *Alisma plantago-aquatica*; *B*, *Brassica oleracea* varieties; *Bv*, *Buddleia variabilis*; *C*, *Sarothamnus scoparius*; *Ch*, *Cheiranthus* (garden varieties); *Cn*, *Centaurea nigra*; *Ca*, *Cirsium arvense*; *Cl*, *Clematis vitalba*; *D*, *Deutzia gracilis*; *E*, *Sambucus nigra*; *F*, *Sinapis arvensis*; *Fa*, *Raphanus raphanistrum*; *G*, *Helianthemum chamaecistus*; *H*, *Hypochaeris radicata*; *Hs*, *Heracleum sphondylium*; *I*, *Ilex aquifolium*; *Im*, *Impatiens roylei*; *J*, *Papaver orientale*; *K*, *Cornus sanguinea*; *L*, *Rubus loganobaccus*; *M*, *Sorbus aucuparia*; *Ml*, *Melilotus arvensis*; *Me*, *Mentha* spp.; *Mo*, *Montbretia pottsii*; *N*, *Prunus lusitanica*; *O*, *Crataegus monogyna*; *Oe*, *Oenothera biennis*; *P*, *Plantago lanceolata*; *Po*, *Polygonum persicaria*; *Q*, *Rubus idaeus*; *R*, *Ranunculus bulbosus*; *Ra*, *Ranunculus acris*; *Rh*, *Rhododendron ponticum*; *S*, *Scilla non-scripta*; *Su*, *Filipendula ulmaria*; *Sc*, *Castanea sativa*; *So*, *Solidago virgaurea* and garden spp.; *Sp*, *Sparganium erectum*; *T*, *Taraxacum officinale*; *Te*, *Tilia europaea*; *Ts*, *Teucrium scorodonia*; *U*, *Allium ursinum*; *Ug*, *Ulex gallii*; *V*, *Vicia faba*; *W*, *Trifolium repens*; *Wd*, Dutch clover; *X*, *Rubus fruticosus* agg.; *Y*, *Epilobium angustifolium*; *Z*, *Ligustrum vulgare*.



Fig. 5



Fig. 6

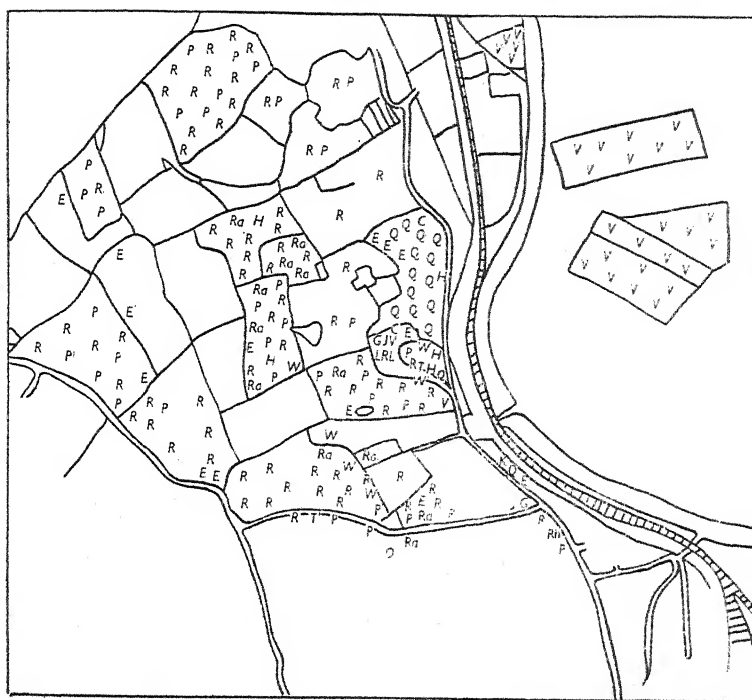


Fig. 9

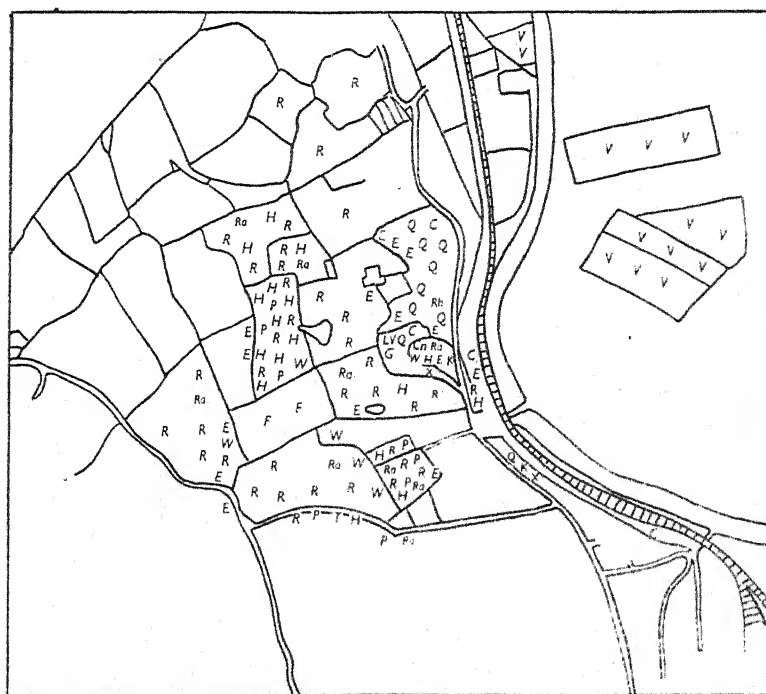


Fig. 10

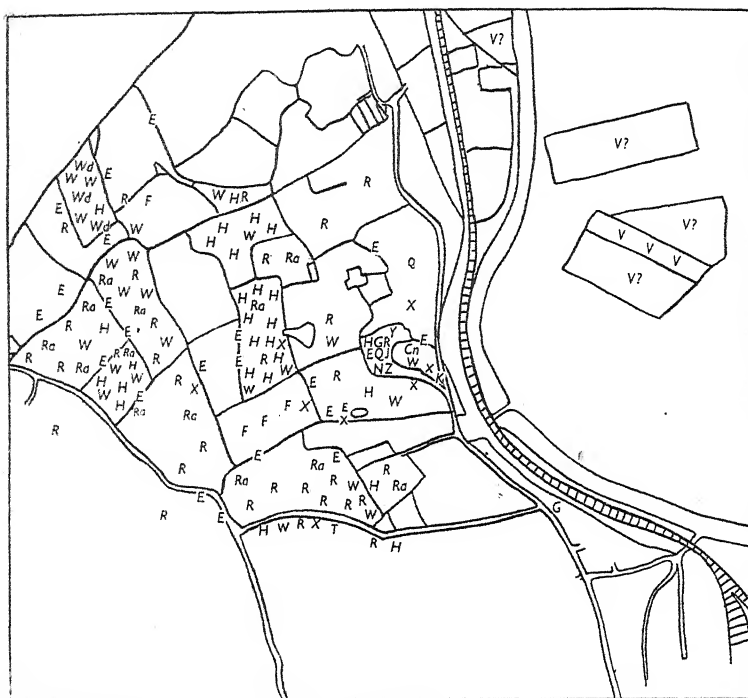


Fig. 11

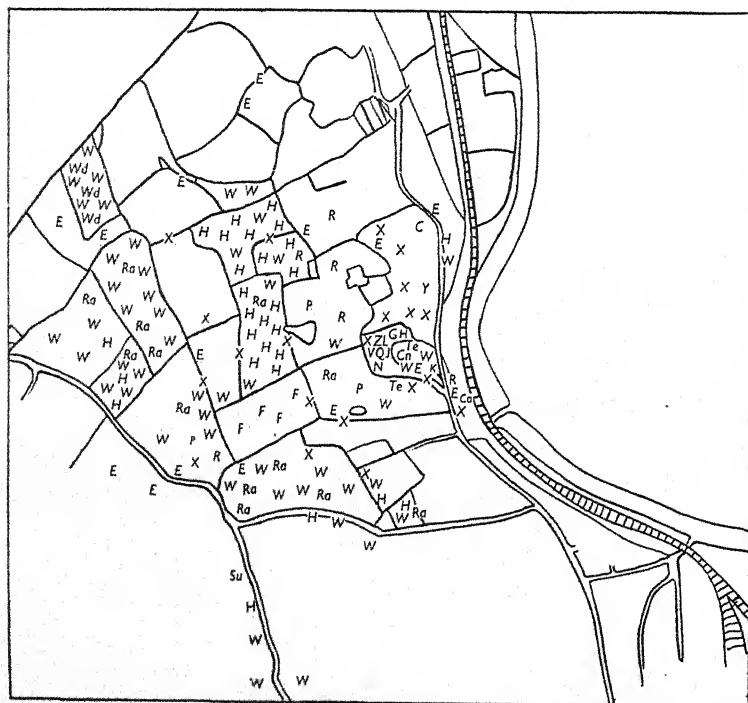


Fig. 12

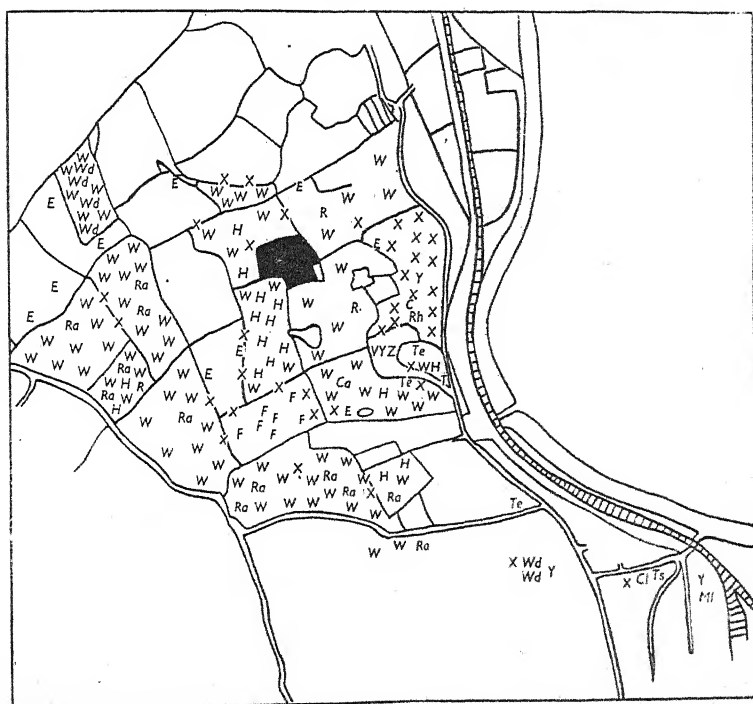


Fig. 13

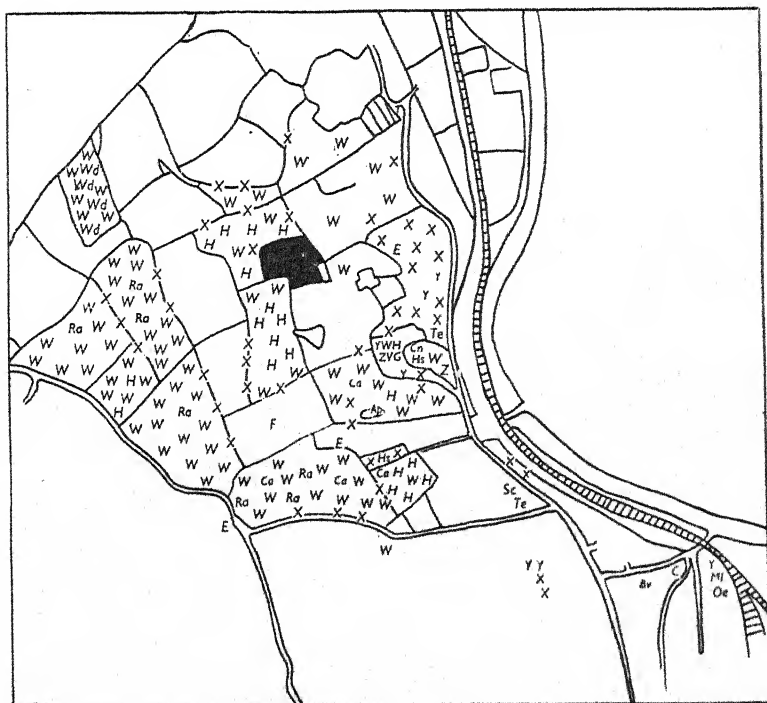


Fig. 14

REVIEWS

THE EVOLUTION OF THE CONIFER CONE

Die Koniferen des Oberkarbons und des unteren Perms, Parts 1-7. By RUDOLF FLORIN. *Palaeontographica*, Stuttgart, LXXXV, Abt. B, Lief. 1 (1938), Lief. 2-4 (1939), Lief. 5 (1940), Lief. 6, 7 (1944).

This work of Florin's is the greatest contribution ever made to Conifer morphology. It makes progress in giant strides and it eliminates many errors. Never before has such wealth of fact been assembled with such profuse illustration, nor indeed has so much been written.

It is a great misfortune that war cut across its publication. It started to appear in *Palaeontographica* the sumptuous Stuttgart publication in 1939 and the first three parts were published before the war and no doubt widely circulated. Parts 4-7 were published during hostilities and very few copies indeed are available; the eighth and last part was in the press and lost when Germany collapsed. I hope it will be published somewhere before long, its loss is particularly unfortunate as Florin is a writer who puts his general conclusions at the end of his work.

This review aims at presenting some of Florin's most interesting conclusions; it is by no means an abstract. An abstract to cover 654 pages and 186 large plates would need to be very much longer. The arrangement is changed: we will begin with the Cordaitales which Florin places near the end of his work, and then consider the Coniferales in the strict sense and finally the Taxales.

(i) *Cordaitales*. Florin's present work deals with certain details of the reproductive organs, but details which are of prime importance. The large male and female catkins (*Cordaianthus*) have long been known, and the text-books describe their gross structure; the axis bears bracts with little axillary reproductive bud-like organs, which, anticipating evidence, I will call 'flowers'. Each 'flower' consists of its axis, a good many sterile scales and a number of sporophylls; the microsporophyll being a scale with terminal pollen sacs, the megasporophyll being a stalk with a terminal seed. In the absence of clear facts there has been great discussion about the relation of these fertile organs (the sporophylls) to the bracts; some holding as Florin does that they are sporophylls and the equivalents of the bracts and others that they are axillary to bracts making even this little bud an inflorescence. A surprising number of intermediate theories have been put forward, and it has not even been agreed that the male and female 'flowers' are comparable.

A few years ago Schoute made a masterly analysis of the published figures of sections of the female 'flowers'. He found he could place all the lateral organs, both scales and seeds, on a single phyllotactic spiral and so he concluded that the whole structure was simple. Florin figures several excellent new sections which fully confirm this for the female 'flower' and he shows that it is equally true of the male 'flower'. In the different species there is some variety in the level of the insertion of the sporophylls; in the female one called *C. zeilleri* the sporophylls are borne at a middle level and there are sterile scales above and below, all in an unbroken spiral. In the male flower, *C. penjoni*, sterile scales and microsporophylls are mixed, but in *C. saportanus* the microsporophylls are confined to and occupy the whole of the upper part of the floral axis.

Florin also brings forward details of the sporophylls which relate them to one another and to the sterile bracts. All three organs have a single vascular bundle. This remains single in the bracts but forks at the apex of the microsporophyll into two or three, and may fork again to supply the cluster of 2-6 pollen sacs. Comparison with *Rhynia* is easy! In the megasporophyll the bundle also forms three, the middle supplies the nucellus, the two lateral pass into the integument which is formed of two clearly marked halves. There is another kind of female flower called *C. williamsoni* which is very like *C. zeilleri* but the megasporophylls are abortive and here there is very little difference between small megasporophylls with a diminutive nucellus and with an integument of the usual two halves, and certain sterile scales which fork at the apex to give a structure very like an integument but enclosing no nucellus. Florin argues that these three branches at the top of the megasporophyll are equivalent to those at the top of a three-branched microsporophyll; but while these three branches or 'telomes' are equal in the microsporophyll, in the megasporophyll only one forms a megasporangium and the outer branches are sterile and enclose it.

All the work so far mentioned is on the French Permian *Cordaites* flowers; but he also figures the little-known English Carboniferous species *C. pseudofluitans*. Here the megasporophylls are

very long, projecting far beyond the sterile scales and they fork repeatedly in all planes and bear several seeds. This condition is regarded as more primitive and it obviously fits in very well to the telome theory.

(ii) *Coniferales*. The *Coniferales* are nearly as old as the *Cordaitales*, as they are known from the Upper Carboniferous: it is their continued existence which makes them seem a much more recent group. Most of the Carboniferous and Permian Conifers were once named *Walchia* which was a very vague and little-known genus. *Walchia* itself is now split into the two rather similar genera *Lebachia* and *Ernestiodendron* and there are numerous subsidiary genera. These two genera occupy the first five parts of Florin's work and in the next two he discusses other Conifers in relation to them, so they are little known no longer. It is their female cones which form the central theme and they shed a light of interest over the whole plants which are otherwise somewhat ordinary, almost dull. Both genera are widespread in the N. Hemisphere and particularly abundant in deposits from Central Europe. Most of the numerous species must have looked like the small-leaved monkey-puzzle, *Araucaria excelsa*, and like it had a strong leader, whorls of main lateral branches and still weaker pinnately arranged branches.

The stem of a '*Walchia*' (probably a *Lebachia*) also resembles *Araucaria* in gross anatomy and in the fine structure of the wood. Unfortunately details are poor, as material is rare and imperfectly determined. The leaves are in general short simple needles, probably with one vein. As in *Araucaria excelsa* the leaves of the main stem are a good deal larger and differently proportioned from those of the main laterals, and those of the secondary branches are different again. A peculiar feature is that the leaves of the leader and main branches in *Lebachia* fork at their apex, and this forking reappears in both genera at the base of the female cone and is continued by all the bract scales. There is another genus of Permian Conifers, *Carpenteria*, in which all the leaves fork and Florin suggests that this is an ancestral trait of the Conifers, but one which is already disappearing from the family in Permian times.

The male and female cones are of considerable size and occupy a similar position, the end of a small branch, but curiously enough their morphological value is quite different.

The male cone is disconcertingly ordinary. It consists of an axis with crowded microsporophylls which have the usual horizontal stalk ending in an expanded, upturned scale, overlapping other scales. There are probably two pollen sacs which arise at the base of the expanded scale and lie alongside the stalk. The whole thing is a simple 'flower' closely comparable with a modern conifer male cone and entirely different from the male catkin of the *Cordaitales*; nor do the microsporophylls approach those of the *Cordaitales*. Indeed in no Conifer (excluding the *Taxales*) is the microsporophyll radially organized.

The pollen however is remarkable. In *Lebachia* the grains resemble those of *Cordaites* in being almost completely enveloped in the large air sac (like a small head in a big tam o' shanter). In *Ernestiodendron* the air sac is a little smaller, being C-shaped and thus exposing front and back as well as the base, rather as in the single-winged Abietinean grains that are sometimes met. It is thus clear that the winged condition is ancient in the Conifers whether or not it is universally ancestral.

The female cone is 5-10 cm. long in both genera and moderately compact, as say, in *Pseudotsuga*. The stout cone axis bears spirally arranged leaves, the bract scales, in whose axils are little fertile shoots called the 'seed-scale-complex' by Florin. Each has a short but distinct stem (even the stem apex has been recognized) and numerous sterile or fertile leaves in a close spiral round it. In *Lebachia* there is a single megasporophyll which arises about half-way up the shoot, on the side facing the cone axis. The sporophyll looks like an ordinary leaf in its lower part, but it soon expands into the base of the single terminal ovule. This ovule looks very like the seed of *Cordaites*, having a similar integument and apical archegonia, but other internal details are unfortunately lacking.

Ernestiodendron has a very similar cone except that instead of a single megasporophyll and many sterile scales there are many megasporophylls and few sterile scales, sometimes none. In some species the seed is erect as in *Lebachia*, but in others the megasporophyll bends sharply and points the seed apex to the cone axis as in so many modern conifers. A seed-scale-complex could hardly look more like an axillary short shoot than it does in these two genera, the most ancient of known conifers. I think that everyone who looks at Florin's figures will feel that no other view of it is possible, and I think that nearly everyone will agree that this short shoot of 'flower' is fully comparable with the female flower of *Cordaites*. The differences between their male organs make it clear however that we have still some way to go before understanding the relation of the Conifers and *Cordaites*.

The seed-scale-complex varies a good deal in Conifers of later periods, in some it resembles a shoot (though never as closely as in the two oldest), while in others it shows no obvious resemblance at all. Certainly as time goes on the shoot-like complexes become less prevalent and Florin marshals his evidence to suggest that there was progressive evolutionary change from a shoot-like structure to a simple looking flat body, the 'ovuliferous scale' of current literature. He holds that in no case is this of the morphological nature of a single fertile scale leaf, and he rejects the term 'ovuliferous scale' as a thoroughly bad misnomer. I fear that the new term 'Samenschuppenkomplex' that is 'seed-scale-complex' is rather long and it may get shortened in the minds of the unsophisticated into just what we started from.

I will select a few examples from the truly amazing series of Palaeozoic and Mesozoic Conifers discussed by Florin.

In the Trias, the oldest stage of the Mesozoic there was once a genus of very prevalent conifers called *Voltzia* but this, like *Walchia*, is now split. *Pseudovoltzia* is one of these new genera. Here the seed-scale-complex resembles a shoot only a little less closely than in *Lebachia*, but it is vertically flattened. Florin believes he can still recognize a decussating sequence in the sporophylls and sterile scales. The sporophylls are described as slender stalks: this differs from earlier accounts where the seeds were thought to be sessile on the surface of certain of the pointed scale leaves. Another fragment of *Voltzia*, *Voltziopsis*, is interesting in presenting a forked bract-scale for the last time, and for its very numerous megasporophylls. *Voltziopsis* has much the same relation to *Pseudovoltzia* as the very fertile *Ernestiodendron* has to *Lebachia*.

We may now pass to the next formation, the Jurassic, where we will select *Cheirolepis*. Here the seed-scale-complex is shaped something like a glove with stubby fingers, though there may sometimes be more than five of the fingers and they may not all be in one plane, and again this is one of the last times that feature of a shoot is met. In *Cheirolepis* the seed-scale-complex has not only flattened, but the different scales are fused or adnate below. Florin does not bother the reader much with the fundamental implications of the idea of morphological fusion, rightly perhaps for the less said the clearer; but he believes that it has played an enormous part in obliterating the evidence of separate scales in the complex. The seeds are held to be borne terminally on slender stalks or sporophylls; here Florin differs radically from Hirmer and Hoerhammer who believed them not only sessile but embedded. Florin has every right to dispute an author's account of the structural facts of a fossil; indeed, he has the duty. In a fossil even major features of external form can be so obscured as to need a good deal of theory to make good sense of them. The disagreement shows that the evidence needs to be more clearly displayed and I feel that the little-used technique of balsam transfers would have helped. As it stands the evidence for the terminal position of the seed on a stalk-like megasporophyll in several of the Mesozoic Conifers seems to me less fully convincing than, say, the case for regarding the seed-scale-complex as an axillary short shoot.

These genera are selected as among the least reduced of their day, but along with them are others which are much more reduced and therefore more modern in aspect. Even as far back as in the Upper Permian there is *Ullmannia* where the sterile scales of the seed-scale-complex are adnate laterally to give a single flat scale with only faint grooves on its surface to suggest its composite origin. In *Elatides* (Middle Jurassic) the adnation has gone further; the single 'cone scale' includes the large bract scale and bears on its upper surface tiny upgrowths (sterile scales) and a little below them are the attachment points of the seeds, all that remains of the free megasporophylls. By Liassic times the more profoundly reduced *Araucaria* cone scale becomes widespread. Here the bract scale, one sterile scale (ligule) and the ovule—all that remains externally of a megasporophyll—are almost completely adnate. Since such varied structures exist the evidence must be marshalled in a particular order and a different case could perhaps be supported by different marshalling, but for my part I find Florin's treatment fair and convincing.

The origin of the modern Conifer families must apparently be looked for rather far back and there is no explicit discussion of the problem; perhaps that belongs to the missing volume. There is, however, an interesting suggestion that the seed-scale-complex in *Cephalotaxus* (just two sporophylls and no sterile scales as a rule) is to be compared with the Mesozoic genus *Palyssia* (with several sporophylls adnate to the bract scale) and with the Palaeozoic *Ernestiodendron*.

We need not follow Florin's full review of the seed-scale-complex in the living conifers; some of his account might be guessed from what has been given above. For instance, *Cryptomeria* with the most elaborate complex comes first, then the rest of the Taxodiaceae, and then other families (where reduction is more severe). In the Abietineae the simple looking 'ovuliferous' scale is

regarded as two or three sterile scales, two megasporophylls and an axis, all fully adnate to one another. In the Podocarps the epimatium is one large sterile scale.

(iii) *Taxales*. Florin's *Taxales* comprises only the four living genera *Taxus*, *Torreya*, *Austrotaxus*, *Amentotaxus* and a few fossils like *Taxus*; (the other genera which some have included such as *Cephalotaxus* and the Podocarps are genuine Conifers, but with feeble cones). Thus defined, the *Taxales* are considered utterly distinct from the Cordaitales and from the Conifers. There is no megasporophyll, the female short shoot has a good many sterile scale leaves and ends by producing a single ovule, terminally on the short-shoot axis.

The fossil history of the *Taxales* begins in the Lower Jurassic with *Palaeotaxus*. This has leaves fairly similar to *Taxus* and very similar axillary fertile short shoots with terminal ovule. A little later there is a plant so like *T. baccata* in details of leaf and female organs that it is included in the living genus as *Taxus jurassica*. These early *Taxaceae* carry the order back as a separate entity and there leave us guessing: they certainly bridge no gap but, as Florin insists, emphasize a gap.

I would only make the following remark in conclusion. Florin's work clears away a great deal of muddle from the Conifers and people will now think alike on the female cone where they thought diversely. I must welcome this because I feel sure Florin is right but I do think that there is a risk people may fail to make personal judgement and use Florin's authority instead. The length of this work and its very excellence may frighten opposition. For example no critic has the right to say that Florin is mistaken over *Lebachia* without digesting several hundred pages of by no means light reading. I hope that there may still be someone who holds that the cone scale is a simple unit structure and that he will bring forward his case. It will be impossible not to admire the steadfastness of this hypothetical critic and sympathy may be extended to him, for Florin is no mean antagonist.

T. M. HARRIS

Plant Life of the Pacific World. By ELMER D. MERRILL. 8×5·4 in., pp. xv+295, 256 text-figs. New York: The Macmillan Co. First printing 1945; second printing 1946. 16s.

This forms a volume of the Pacific World series, published under the auspices of the American Committee for International Wild Life Protection; according to the bibliography of Dr Merrill as published in *Merrilleana*, it has also appeared as a 'Fighting Forces edition, Infantry Journal, Washington, D.C.' Both in the United States and elsewhere manuals were provided for the Army, mainly with the object of giving information about animal and plant life in exotic places, especially with regard to useful or poisonous products. Under the heading 'Jungle foods' the author refers to a number of books on this subject, among these his own *Emergency Food Plants and Poisonous Plants of the Islands of the Pacific*, published by the War Department in 1943. The present volume has a much wider scope. It is an extremely stimulating handbook for any man with an interest in botany who happens to spend part of his life in the tropics of the Pacific. Many popular books on botany exist, describing 'the flowers' of this region or that, but most of them are of strictly local interest and few if any deal with the tropics. Dr Merrill covers the enormous space of the insular world of an ocean. The description of vegetation and flora, their composition, biology and distribution, actually applies with few exceptions to the tropical and subtropical belt only, but in the Bibliography reference is made also to the far north and south. For some reason or other Easter Island and the Juan Fernandez group have been excluded. In my opinion they have at least the same right to be mentioned as the Aleutian Islands, where we are outside the limits of all Pacific floras.

The book has not, the author says, been prepared for the professional botanist. This is of course true, for what he tells us under 'General Principles of Botanical Classification' was certainly written for the layman, and every college student is familiar with many of the common cultivated plants described and illustrated as well as with insectivorous plants, strangling figs, huge *Rafflesias*, etc. On the other hand, even the professional botanist will find here much of information on a region of which few have personal experience and none a wider outlook than the author. His book is a useful manual for everybody who chooses to devote himself to the botany of the Pacific. Nobody should start work there without having read it, and as his studies progress he will undoubtedly consult it very often, for it is full of facts and sound reasoning. Moreover, it is pleasant reading. The various types of vegetation, seashore, mangrove, primary and secondary lowland forest, montane forest,

grasslands, etc. are ably described and their characteristic elements presented in good pen-and-ink drawings. A special chapter deals with the weeds and their significance; no less than 78 species of this category are figured. Another is devoted to the cultivated plants, both edible and ornamental, and equally profusely illustrated. Of particular interest is the discussion of the problems of distribution and, in this connexion, the local names and what they tell about origin and dispersal of a number of important species. Whereas, in a way, the history of the Malaysian flora proper may be fairly well understood, the distribution in Polynesia has given birth to much wild speculation. It is gratifying to the reviewer that Dr Merrill gives full stress to the fact that the biological alliances of the remote Pacific islands are overwhelmingly with the western Pacific, and also that he hints at the Tertiary Antarctic flora as another source. How long-distance dispersal can be explained is the crucial point if we take it for granted—which the author does not, however, even if he is no friend of land bridges—that the present distribution of land and sea has undergone no material change since the beginning of the Tertiary. He admits that dispersal agencies, as we know them, account only for a number of shore species and wind-borne cryptogams, but even where circumstances are as favourable as with the spore plants we meet with difficulties.

Brief notes on the history and exploration of the Pacific flora, a selected bibliography, an experienced collector's directions for preparing specimens, a list of species arranged systematically, a glossary and an index complete this useful, cleverly composed and extremely well-written volume.

C. SKOTTSBERG

Merrilleana, A Selection from the General Writings of ELMER DREW MERRILL, Sc.D., LL.D. *Chronica Botanica*, vol. 10, no. 3/4. Edited by FRANS VERDOORN. 10.3 × 6.8 in., pp. 131–393, 3 plates, 10 text-figs. Waltham, Mass.: Chronica Botanica Co. 1946. \$4.00.

It is customary for colleagues, pupils and friends of a prominent scientist and teacher to contribute to a dedicatory volume when he passes a notable milestone, and Dr Merrill's 70th birthday and his retirement from the directorship of the Arnold Arboretum made no exception to this rule (see the *Journal of the Arnold Arboretum*, vol. 27, no. 4). It is much less common that he is celebrated with a reissue of his own writings, but this unusual honour was also bestowed on Dr Merrill. *Merrilleana* includes a foreword by the Editor, a *curriculum vitae* with appropriate illustrations, a complete bibliography comprising 488 titles, and 23 papers. It is not intended to reflect Dr Merrill's activity as a taxonomist, manifested by a large number of books and papers of fundamental importance to our knowledge of Indomalaysian vascular plants, notably those of the Philippine Islands, where he inaugurated a new era of research. The 23 papers selected are classed as 'general writings'. Dating from 1907 to 1946 they bring forth the wide scope of Dr Merrill's interests, embracing phytogeography, the history of cultivated plants, early, little known and badly interpreted systematic works, economic botany, ethnobotany, technical questions, etc., and they give us a clear insight into the rare qualities of a prominent scientist and excellent writer, his sharp intellect, vast first-hand knowledge, critical mind and logical reasoning.

The first article, 'The Ascent of Mount Halcon' (in Mindoro), shows us the man in the field, facing severe hardships and succeeding where others had failed. Several papers, beginning with 'Amboina Floristic Problems', illustrate the enormous amount of time and labour Dr Merrill has devoted to the interpretation of the writings of Rumphius, Loureiro and the erratic Rafinesque, works that on account of their troublesome nature or rarity or both had remained widely neglected, misinterpreted or even practically unknown. He has cleared hundreds of genera and species, most of which never found their way to *Index Kewensis*. His book on Loureiro's *Flora Cochinchinensis*, from which parts of the introductory chapter are reproduced, will ever remain indispensable to all students of the Malaysian flora. The same holds good for his catalogue of Bornean plants and his 'Enumeration of Philippine Flowering Plants'; in both cases excerpts from the introductory chapters are given, also reflecting another side of Dr Merrill's activity, his important contributions to phytogeography. This is true also of 'Die pflanzengeographische Scheidung von Formosa und den Philippinen', where he showed that these two regions belong to different botanical provinces. In 'Correlation of the Indicated Biological Alliances of the Philippines' he deals with the geological history of Malaysia and its bearing upon the regional distribution of various floral elements over the island chains from Sumatra to New Guinea. Based on a large statistical material he explained

the alliances between north and south and east and west, reconstructed the paths followed during different epochs and interpreted the significance of the Wallace and Weber lines.

A topic of general interest to which Dr Merrill has given much attention is the origin and history of tropical food and other useful plants. On historical, botanical and linguistic grounds he refuted O. F. Cook's theory of the American origin of such widespread plants as *Cocos nucifera* and *Hibiscus tiliaceus*, he returned to them in his 'Significance of Oriental Plant Names', where he proved the American parentage of the Frangipanni and followed its history in cultivation. During these studies he became confronted with the two fighting schools of ethnologists, the 'modern conservatives' and the 'extreme diffusionists'; the latter built up bold theories on the basis of assumed cultural similarities and claimed Egypt as the sole primary centre of agriculture whence it spread east and west across hypothetical sunk land masses. It is gratifying to follow Dr Merrill's sober criticism in papers like 'Scuttling Atlantis and Mu', 'Domesticated Plants in relation to the Diffusion of Culture', or 'Further Notes on Tobacco in New Guinea'. There is little left of the extreme diffusionists after he has dealt with them and given convincing proofs of the independence of American culture. In 'Man's Influence on the Vegetation in Polynesia' he discusses the weed flora and its bearing upon the problems of dispersal. Under the somewhat puzzling title 'Some Economic Aspects of Taxonomy' reappears the brilliant paper he read at the 75th anniversary of the Torrey Botanical Club. He tells the amusing story of the controversy between Torrey and Eaton, he emphasizes the necessity of critical taxonomic treatment of economic plants, he gives an estimation of the number of known plant species and he winds up with a plea for a just recognition of the basic value of systematic botany: 'laboratory people should realize the importance of accurate identification'.

It goes without saying that during his systematic work Dr Merrill has been confronted with innumerable questions of nomenclature. His interpretation of Rumphius and Loureiro have caused many changes, received with little enthusiasm by conservative students. His revival of Rafinesque will give rise to much confusion if we cannot agree to conserve names of current usage. His paper on the validity of William Bartram's binomials is reproduced.

As an editor of publications and a curator of collections Dr Merrill always had his eyes open for useful reforms. Papers like 'An Appeal for Simplified Literature Citations', 'A Simple Change in Name', 'One-named Periodicals', 'On the Technique of inserting published Data in the Herbarium', and 'Index Kewensis in Improved Loose-Leaf Ledge Form', give a glimpse of his inventory genius in practical matters.

Merrilleana is a well-produced and extremely readable book; Dr Merrill's style is clear and concise and seasoned with the slightly sarcastic humour his many friends have learnt to appreciate. Among the illustrations are decorative vignettes of four genera and a couple of species named after Dr Merrill, and an excellent portrait of the busy Director of the Arnold Arboretum.

C. SKOTTSBERG

Forest Soils and Forest Growth. By S. A. WILDE, F.E., D.TECH.SC. Pp. xx+203, with bibliography, indices and 7 plates. Waltham, Mass.: Chronica Botanica Co.; London: Wm. Dawson and Sons Ltd. 1946. Price \$5.00.

This book is No. 18 of the now well-known 'New Series of Plant Science Books'. As the title implies, the author has a very different aim from that of writing a text-book on forest soils. He takes the view that soil and vegetation are one unit, so that silvicultural practice should be related to soil properties, and soil properties are in their turn influenced by silvicultural treatment. This attempt to bring together the two points of view—the theory of soil science and the practice of silviculture—makes the book completely different in scope from previous text-books on either soil or silviculture which are available in the English language. It has led the author to range over a great variety of subjects, and to treat many of them rather superficially; the book as a whole suffers from undue compression.

It was based on lectures for 'a rather heterogenous group of students, including graduates and upper classmen in soils, forestry, botany, game management, and landscape architecture'. It is also evident from the many technical details given (e.g. rates of application of fertilizers, analytical methods, etc.) that the author has attempted to produce not only a text-book for use at the University, but also a handy reference book for use in later life by these students in their varied professions.

The first part of the book (pp. 1-126) describes forest soils and their properties; it includes

chapters on forest vegetation, soil organisms, forest humus and forest types. The second part of the book (pp. 127-203) is devoted to forestry practice in its relation to soils, and includes chapters on such subjects as soil survey, planting practice, thinning and felling, the productivity of forest soils, and the treatment of soils in nurseries.

The first 56 pages are devoted to the description and classification of the major soil groups of the world in relation to climate and vegetation. In several respects this is an advance on previous treatments of the subject, and is by far the most useful and valuable part of the book. The treatment of tropical soils is fuller than usual. Several new terms and conceptions of soil groups are introduced. Thus the terms 'brown earth' and 'brown forest soil' are discarded in favour of 'melanized soils'; it would have been useful to have a fuller discussion of the reasons for this change, and of the difference between the older and the newer groups. The Russian folk-name 'Grood soil' is introduced into English literature to designate a group of 'nut-structured prairie-forest soils' which have formerly been known as 'grey forest soils', 'degraded chernozems', etc. The 'Charal' soils characteristic of the regions of sclerophyllous 'Mediterranean' vegetation are another new group. The use of terms such as 'alkaline raw humus' and 'podzolized rendzina' will seem strange to many soil workers, though in this case it is perhaps more a difference in definition of terms than an introduction of new concepts. In view of these deviations from traditional treatment, it seems a pity not to have devoted much more space to this part of the book, especially since it is obvious that a very wide knowledge and much careful thought have been employed in this serious attempt to improve and reconcile earlier classifications of world soil groups.

The chapters on physical and chemical properties of the soil are disappointing; the treatment follows traditional lines, and makes no mention of several important advances of recent years, such as the use of redox potential and capillary water potential. pH is treated as though it was a fundamental and important property of the soil, instead of merely a property which is conveniently measured, but the meaning and interpretation of which are still extremely obscure. There is also a tendency both in these chapters and in the later part of the book to assume a far fuller understanding than we actually possess of the relationship between the nutrient status of the soil and its productivity. Despite statements such as those on p. 75, it is still notoriously impossible to relate the productivity of a forest soil to its measurable chemical and physical properties, with any degree of precision.

The second section of the book makes excursions into many subjects, including forest valuation, economics, mensuration and silviculture. It is impossible for the reviewer to assess the value of this matter for the American students for whom it is written, but he cannot help feeling that the author has not achieved his main object through failing to come to grips with the fundamental principles involved, at the expense of a large mass of comparatively unimportant detail, particularly detail of a technical nature. Much of this may, of course, be of value to the practitioner, though not to the student. A great deal of the matter relates tacitly to American conditions, and the value of this part of the book is still further restricted by a strong tendency to reduce silvicultural practice to a series of recipes and rules, such as that relating suitability for planting to soil texture (p. 66). Such rules have, of course, their value, as representing attempts to summarize our theoretical knowledge in a practical way, but it cannot be too strongly emphasized that they are bound to be of local application. The 'practical man', away from the influence of his university, is far too apt to forget how to make his own applications of his theoretical knowledge and to follow such rules blindly; they are a prolific source of silvicultural mistakes. The author gives few warnings of their limitations; indeed he often gives no indication of the part of the world in which a particular technique which he describes has been evolved or applied. Many of the technical details given—e.g. those relating to the preparation of yield tables, compound interest formulae, and formulae for calculating annual yields—are unnecessary for the discussion of the principles involved; they are of no interest to the non-forester, and they are quite inadequate for the needs of the Forestry student, for whom each of these topics must form but a small part of a much more extensive course of study. Of the later chapters those dealing with nursery practice will be of most value to English readers, since they suggest a technique of deliberate maintenance of nutrient status, base exchange capacity, etc., at desired levels by applications of organic and inorganic fertilizers on the basis of soil analyses—a procedure which has probably never been followed in any British forest-nursery. But once again there is no adequate discussion of the basis of this kind of treatment—how for example the desired levels of nutrient status are to be determined—and many would consider that the procedure is based on views of tree nutrition which are not yet fully established.

There are in addition a number of minor criticisms to be made. There are many statements in all parts of the book which are either misleading or not quite accurate. For example, fungi are not necessarily multicellular organisms (p. 98); the definitions of 'high moor' and 'low moor' are incorrect (p. 32); there is confusion between the magnitude of the figure for pH and the degree of acidity (p. 37); shelter-wood strip fellings were *not* originated by Wagner (p. 160) though the particular form described is Wagner's. There are several discrepancies between dates of papers as cited in the text and as given in the bibliography, and a number of misspellings of plant names. Some of the references cited in the text bear no relation to the subject in connexion with which they are given—e.g. Burger's *Holzarten auf verschiedenen Bodenarten* (1931, p. 118), does *not* deal with soil-forest types. Fuller explanation is needed for several of the diagrams—e.g. Fig. 9 showing the relation of forest-type to site is difficult to understand because only isolated clumps of trees—symbolic of the forest type—have been shown, when in fact they represent a region of continuous forest.

Despite these faults a tremendous mass of material has been brought together into a small space, and the serious worker should find many useful suggestions and references. E. W. JONES

Report for the War Years. Rothamsted Experimental Station. 9½ × 6 in. Pp. 270. Gibbs and Banforth. St Albans. 1946. Price 5s.

The Rothamsted Annual Report was not issued during the war and an inclusive one covering the years 1939–45 has now been prepared. It surveys an immense range of activities, some of them relating to war-time problems such as the effect of lethal gases on crop plants. Summaries of numerous published papers are included with the reports from the individual departments and sections ranging from soil physics to bees and including botany, crop physiology and plant pathology. These are obtainable separately at 1s. W. O. JAMES

Biologia. Edited by F. VERDOORN. 15 × 8½ in. Waltham, Mass.: Chronica Botanica Co. 1947. Biannual subscription \$4.00.

A monthly newsletter to be published under this title as a supplement to *Chronica Botanica* whose regular subscribers will receive it free. It is to be small and informal and will give brief reports of developments of a professional and international interest. The first number, dated January 1947, has numerous notes of recent publications; recent and forthcoming congresses and personalia. W. O. JAMES

The Natural Vegetation of Trinidad. By J. S. BEARD. 10½ × 7½ in. Pp. 152 + 14 plates, 19 text-figures and one folding map in colours. Oxford Forestry Memoirs, No. 20. 1946. Clarendon Press, Oxford. Price 20s.

The island of Trinidad is about the size of a large English county and lies between 10° 3' and 10° 44' north latitude; it has a much richer flora and more diversified soils and vegetation than most areas of similar size. Unlike the other West Indian islands (excepting Tobago), it is not volcanic and is structurally part of the South American continent, from which it is separated only by narrow straits. Botanically it is comparatively well known and it is therefore very satisfactory that Dr John Beard has been able to add a comprehensive account of its natural vegetation to his long series of useful papers on West Indian vegetation.

The classification of the plant communities follows the lines put forward in an earlier paper (J. S. Beard, 'Climax vegetation in tropical America', *Ecology*, 25, 127–58, 1944). Eight climatic climax formations and seven edaphic formations are recognized. The moist evergreen forest formation of the Trinidad lowlands experiencing a drought of about 3 months (3 successive months with less than 4 in. rainfall) Dr Beard terms 'Evergreen Seasonal Forest', reserving the term 'Rain Forest' for the evergreen forests of the Montane and Lower Montane regions which are not subject to drought. 'Evergreen Seasonal Forest' differs from 'Tropical Rain Forest' (in this restricted sense) in having a discontinuous, instead of a continuous, highest tree story. The distinction between the two types is undoubtedly useful, but if 'Tropical Rain Forest' is defined as narrowly as Dr Beard proposes, probably very little of the Rain Forest belt of the tropics will prove to be 'true rain forest'. The Mora forest of Trinidad, a remarkable forest type in which a single species, *Mora excelsa*, forms 85–90% of the trees in the 'canopy layer', is now regarded by the author as a 'faciation' of the mixed Evergreen Seasonal Forest association, not (as in his 1944 paper) as a true

rain-forest community; thus none of the evergreen forest types of the Trinidad lowlands is now classified as a rain-forest formation.

All the communities are described with a wealth of precise physiognomic detail which adds much to their value for comparative purposes; stratification is shown by means of excellent profile diagrams and statistics are given of the proportion of deciduous species in different strata, of leaf sizes according to the Raunkiaer classification, percentage of buttressed trees, etc. Floristic composition is shown by tables giving the estimated average composition per 100 acres of each of the forest types. Though most of the work is devoted to climax communities, there is a short account of secondary vegetation and secondary successions. The distribution of the chief plant communities on the Crown Lands (which include most of the remaining forest on the island) is shown on a large map in colours. A section of the work entitled 'Flora' includes a short history of botanical collecting in Trinidad, the regional affinities of the flora and a complete list of native trees.

To the ecologist not specifically concerned with tropical vegetation or the West Indies, the most interesting parts of the book will probably be those dealing with the savannas and with the historical evolution of the plant communities in Trinidad. Though the island was at one time almost entirely forest-covered—in 1802 only some 10 % of the land had been brought under cultivation and even to-day 22.7 % of the land area is reserved forest—savannas, apparently of natural origin, are found in several small isolated areas and the vegetation of these is exceptionally interesting—that of Aripo savanna with its *Drosera*, *Utricularia* spp. and *Sphagnum* has long been well known to botanists. Dr Beard shows conclusively that the Trinidad savannas cannot be climatically determined, since they occur as small pockets in forested areas. Modern opinion seems to be inclining to a similar conclusion for all tropical savannas, since all of them exist in climates in which forest can probably develop given suitable soil conditions; Schimper's 'Tropical Grassland Climate' thus has no foundation in fact. Dr Beard also rejects the view (at least for the majority of the Trinidad savannas) that savannas are necessarily biotic climaxes due to recurrent fires. The Aripo savannas, for instance, have never been known to burn, yet show no tendency to revert to forest. The rich flora of the Aripo and Piarcó savannas, which includes several endemic species, also supports the view that they are a type of vegetation of great antiquity and not recently derived from the destruction of forest. Dr Beard suggests that these savannas occupy relics of a Pleistocene land surface formerly continuous with the *llanos* of Venezuela; elsewhere in Trinidad this old senile land surface has been eroded and its soils regenerated. The persistence of the savanna vegetation is probably due to special soil conditions preventing the growth of forest—impeded drainage giving rise to alternate water-logging and drought in the case of the Aripo and Piarcó savannas, shallowness of soil over a parent rock which weathers with difficulty in the case of the hill savanna at St Joseph. A further paper on the savanna problem which Dr Beard promises will be awaited with great interest.

Dr Beard, like almost all workers with an intimate acquaintance with tropical vegetation, is not satisfied with Clements's conception of the climatic climax. He finds, for example, that limestone ridges in Trinidad bear Semi-evergreen Seasonal Forest quite distinct from the Evergreen Seasonal Forest which is clearly the climatic climax of the lowlands. No imaginable change of soil conditions would convert these limestone soils into the clays or sands necessary for the development of Evergreen Seasonal Forest. Dr Beard also criticises the concept of the edaphic climax as used by British ecologists on the grounds that the same community must be regarded as an edaphic climax in one place and as a climatic climax in another. Thus Semi-evergreen forest which in some parts of Trinidad occurs as an edaphic climax on limestone ridges in regions with a drier climate, occurs as a climatic climax even on optimum soils. There is much evidence to support the view that the most important factor determining the nature of the vegetation in the tropics is the moisture-supplying ability of the soil—itself determined by several factors among which climate is only one.

Dr Beard believes that the vegetation of Trinidad is passing through a cycle of changes which have led to the establishment in the lowlands on soils with optimum water-supplying ability of Evergreen Seasonal Forest. This is the up-grade phase of the cycle; it will be followed by a down-grade phase in which the Evergreen Seasonal Forest will be replaced by Marsh Forest and savanna as soils and topography become senile. The present developmental cycle was initiated by the uplifting of the land in recent geological time and the consequent rejuvenation of the landscape; the relict savannas bear witness to the senile stage of the previous Pleistocene cycle. Regarding the climatic climax in the light of this theory, Dr Beard thinks it can best be regarded as a formation

which will appear in the development of any ecosystem; it is the highest type of vegetation that can develop under a given climate *the other environmental factors (land-form, soil) having developed the most favourable moisture conditions possible to them in the cycle*. 'As so defined, the climatic climax will not necessarily be the highest type which can exist in the given climate, for such a type would only appear in the presence of ideally favourable conditions of soil and topography. This definition permits of the existence of more than one equivalent climatic climax within a given climate, according to differences in the land-form/soil complex' (p. 146).

Dr Beard's views on vegetation cycles and the climax are obviously highly controversial, but enough has been said to show the wealth of interest in his book. The vista of interesting developments in ecological theory which it opens up support the reviewer in his belief that the study of tropical vegetation will ultimately transform our present ecological concepts and theories which hitherto have been based too largely on the floristically impoverished and mainly anthropogenic vegetation of the north temperate regions.

P. W. RICHARDS

Dating the Past: An Introduction to Geochronology. By FREDERICK E. ZEUNER. $8\frac{1}{2} \times 5\frac{1}{2}$ in. xviii + 444 pages, 101 text-figs, 24 plates. London: Methuen. 1946. 30s.

No one reviewer is likely to be found competent to assess all parts of Dr Zeuner's book, and any reviewer must soon be aware of this. It is, however, the width of the scientific fields considered by the author that gives the very special value to this book and to the integrations which have been attempted therein. Increasingly all the biological sciences, and indeed even the physical sciences are convinced that present phenomena must be explained in terms of the history that has shaped them. This has long been the mainspring of geological science, but botany and zoology (especially upon the ecological, taxonomic and phytogeographic sides), archaeology, climatology and pedology increasingly accept the value of this approach, and all these sciences conjointly afford valuable evidence of the course of the world's history.

Dr Zeuner's book is devoted to an exposition of all the methods which have developed in recent times to date the various stage of the earth's history. Although some attention is given to dating the Archæan, Palæozoic and Mesozoic periods, especially by Radioactivity measurement, the great bulk of the book is devoted to the dating of the Glacial, Interglacial and Post-glacial periods—that is to say, approximately the last million years, the time during which man has been in existence, and during which the genera of plants and animals to-day have been in existence, though not in their present distribution.

This emphasis is natural since the need for Geochronology becomes more urgent as we approach the existing conditions, and as the need for finer scaling makes the zone-fossil methods of the older deposits inadequate. In this period of the last million years many tremendous and even convulsive events have shaped the world. There have been a number of glacial phases, each of which had great repercussions, absorbing water from the world's oceans into polar ice-caps, which locally depressed the earth's crust beneath them, and which strongly affected regional climatic distribution. Such glacial phases were separated by milder interglacials in which sea-level rose and compensating earth-crust tilts took place. The alternation of climate was matched not only by sea-level changes with creation of raised beaches, submerged land surfaces and river terrace systems, but by weathering and erosion and deposition phenomena by wind, sea and air. The climatic shifts forced great vegetational movements across continents and up or down mountain ranges. With the plants moved the animals, and in both groups, much extinction and complex distribution pattern ensued. How far it was directly evocative of evolution of new species we are still uncertain, but these events certainly concerned continuously evolving populations. This is nowhere more evident (or more interesting to us) than in the case of man himself, and this animal may be sketchily traced by his bones and artefacts through this period.

It will be recognized that the final valid geochronological scheme for this long period is one which takes account of data from these many fields of scientific investigation and continues them without conflict into a smooth whole. This aim is far from realization and many workers will feel that it is not going to be brought closer by so large a degree of acceptance of the Milankovitch hypothesis of the cause of the climatic alternations of the Great Ice Age. It may be doubted whether everyone would concede that through Milankovitch's work 'an indisputable factual basis was at last secured for the re-interpretation of the influence of the perturbations on the terrestrial climate'.

The principal methods of geochronology dealt with in the book are tree-ring analysis, so effectively developed by Douglass in North America, varve-analysis, which we owe to de Geer, pollen analysis which has been developed by von Post in Scandinavia, the geological evidence of former changes of land- and sea-level, archaeological evidence, and geological evidence of all categories, and especially the radioactivity measurements applied to rocks of different geological formations.

The introduction here provided to these techniques will be of great value to all concerned with the evidence of the past. The *tour de force* of the book is certainly the handling of the chronology of the past million years, and here the author comprehends a tremendous scope of evidence of all kinds and attempts syntheses. His knowledge of the field evidence and of the literature is vast, and the very extensive bibliography reflects this.

The concluding chapter of the book is headed 'Biological Evolution and Time' and we read 'the significance of geochronology for studies in the evolution of life can hardly be overestimated' and 'it is intended to show... that promising possibilities are contained in a combination of geochronological and palaeontological investigations'.

It is evident that approximate absolute values for the ages of the great geological formations, give a useful scale against which to view the palaeontological evidence of the character of evolution. Numerous interesting instances, such as the fossil history of the elephants, are discussed, but the conclusions are not very closely concerned with time and their validity or falsity hardly concerns the absolute rate. To some degree in this chapter it is difficult to make contact with the drift of the author's mind. His conclusions 'No instance, however, is yet known of a species developing at a faster rate than that found in the elephants (about 500,000 years)' and 'In evolution the number of generations appears to be less significant than the absolute time' certainly are such as to give pause to biologists familiar with other lines of evidence.

H. GODWIN

La Culture des Tissus. By R.-J. GAUTHERET. (L'Avenir de la Science 21.) Gallimard. 1945. Pp. 202 + 32 plates. 190 francs.

It is only recently that botanists have succeeded in growing isolated plant tissues. The culture of these tissues differs from that of animal tissues in two important respects. Plant tissues can be cultivated on exclusively synthetic media. They are rarely true tissues in the strict sense of the word, but usually show some cellular differentiation and may easily be induced to produce plant organs such as leaves or roots.

This is the second book to be published dealing exclusively with the subject of plant tissue culture. It is a useful addition to botanical literature because the technique of growing plant tissues in artificial culture has advanced rapidly in the last 15 years, mainly in the hands of French and American workers. Much of the later work, carried out in France during the war, has only become easily available with the publication of this volume.

In the opening chapters the development of the technique is traced from the first experiments of Haberlandt and others, and the methods now used in the isolation and cultivation of plant tissues are described. The major part of the book is devoted to a description of the morphological and anatomical structure of cultures during their development under various conditions, including observations on many types of tissues from a great variety of species of plants. More especially has Gautheret been interested in the action of heteroauxins and related compounds on the development of plant tissues. The effects produced by these substances are very remarkable. Gautheret shows that their action varies greatly with the tissue and the concentration of auxins supplied. He distinguishes five modes of action of auxins usually apparent at distinct concentrations, namely, cellular elongation, cellular multiplication, root formation, bud inhibition and isodiametric increase in size of cells. The fact that the latter three of these effects occur at concentrations of auxins greater than those encountered under physiological conditions suggests, as Gautheret realizes, that in the living plant factors other than auxin distribution must play a part in development. There is no doubt that experiments using the tissue culture technique will add considerably to our understanding of organ and cell differentiation, and the action of auxins, as occurring in the intact plant.

The later chapters of the book give an account of some aspects of the physiology of plant tissue cultures. Unfortunately no list of references, which would enable the reader to find detailed accounts of the experiments, is included.

The volume is well illustrated. It should interest biological workers in many fields.

J. D. SMITH

OBSERVATIONS ON SOIL ALGAE

III. SPECIES OF *CHLAMYDOMONAS* EHR. IN RELATION
TO VARIABILITY WITHIN THE GENUS

By J. W. G. LUND

Freshwater Biological Association, Wray Castle, Ambleside

(With 3 figures in the text)

A. INTRODUCTION

During the study of British soil algae a number of *Chlamydomonas* spp. were observed and some identified. They were studied by direct observation and cultures using the methods described in Lund (1945, pp. 198-200). Certain characters generally used for specific delimitation were found to be variable, while others were constant. After the work was concluded, it was found that Gerloff (1940) had come to similar conclusions on the basis of a much more detailed study. Earlier work (Moewus, 1933; Czurda, 1935) on specific variability had given contradictory results.

B. THE CELL CHARACTERS AND THEIR SPECIFIC IMPORTANCE

Moewus (1933), using cultures, found that a number of species (especially *C. eugametos* Moewus) show a wide variation in structure even as regards features commonly considered as of taxonomic importance (e.g. papilla, chloroplast and stigma). Fritsch (1935, p. 81) has criticized Moewus's assumption from this that a number of supposedly distinct species are really not separate from one another. Czurda (1935, using *C. eugametos* Moewus) and Gerloff (1940) repeated Moewus's experiments and failed to substantiate his conclusions. Czurda considered that features such as the size and shape of the cells, type of papilla, stigma and chloroplast, together with the number and position of the pyrenoids are suitable characters for specific delimitation. Gerloff reached similar conclusions, though he showed that considerable variation may occur from a basic type dominating a population. Both these authors stress that material containing healthy and actively multiplying cells must be used for diagnoses. The present position may be summarized as follows, examples being taken from Gerloff (1940) and my own observations.

(1) The shape of the cell alters with age. Young are generally relatively narrower than old cells. This is particularly marked if freshly liberated daughter cells are compared with cells which are in the process of division (cf. *C. oblongella* n.sp., Fig. 2 L-P) or those which have become non-motile and lost their flagella (Fig. 2 Q). Due to mutual pressure within the mother cell, developing daughter cells are often asymmetric, one side being flat or concave and the other convex. This asymmetry may persist after liberation but is commonly lost as the cells enlarge with age (*C. Muriella* n.sp., forma C, Fig. 2 BB-FF; *C. parvula* Gerloff, 1940, p. 382, text-fig. 36).

(2) Species lacking a papilla never produce one under any condition. Species possessing a papilla may lose it under certain conditions, notably in relation to size, age and non-motile stages (*C. Snowiae* Printz., Fig. 1 B-H). The type of papilla is constant in any one

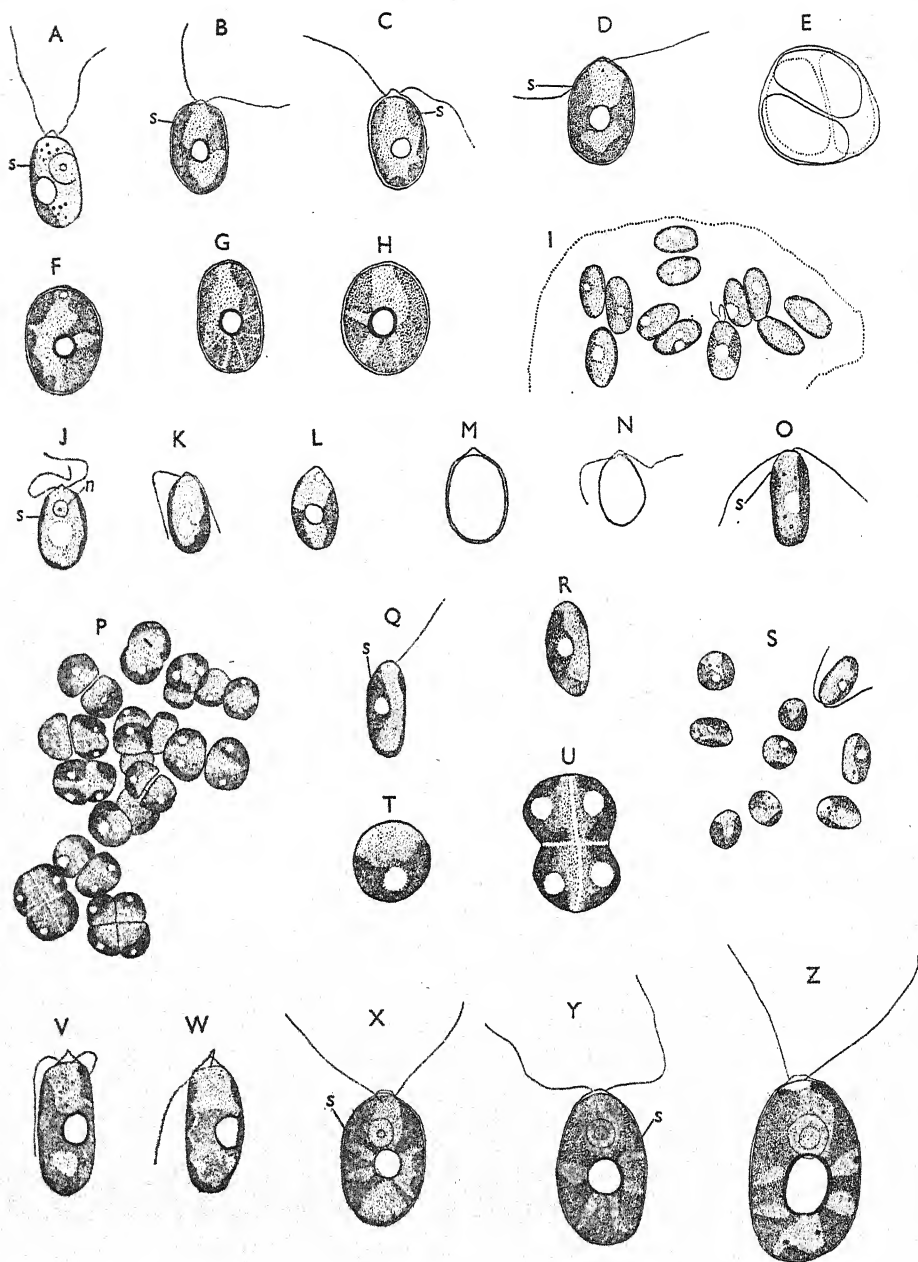


Fig. 1. A, *Chlamydomonas pseudo-elegans* Fritsch & John var. *minor* n.var.; B-H, *C. Snowiae* Printz; I-N, var. *palmelloides* n.var.; O-U, *C. tetras* n.sp.; V, W, *C. pyramidalis* n.sp.; X-Z, *C. macrostellata* n.sp. M, N, stained in fuchsin and gentian violet; F-I, P, S-U, non-motile and division stages. Pyrenoids shown as clear areas in this and succeeding figures. *n*, nucleus and *s*, stigma in all figures. A-E, J-N, P, V, W, X, $\times 1000$; F-H, Y, $\times 1250$; I, S, $\times 730$; O, Q, R, T, U, Z, $\times 1500$.

species, though it may vary in size and prominence even in young motile cells (Gerloff, 1940, text-figs. 11, 12, pp. 338-9).

(3) The number of contractile vacuoles is constant. In most species there are two anterior ones lying in a plane perpendicular to that of the flagella. Only one anterior, or three or more in various positions may occur.

(4) The presence or absence of a stigma is constant. When present, it has a definite location (e.g. anterior or posterior) and form in the majority of cells; in the minority it may be variable in both these characters (*C. stellata* Dill, Gerloff, 1940, text-fig. 24).

(5) The position of the nucleus is not constant. It is related to the development of the chloroplast. Thus, it may be anterior or posterior to the chloroplast bridge in the subgenus *Agloë*. In the majority of cells in a population the location is the same (e.g. anterior in *C. mutabilis* Gerloff, 1940, text-figs. 41, 42, pp. 397-9).

(6) The chloroplast varies from a basic shape which is present in the majority of the cells in a population. Thus, a species of the subgenus *Chlamydeella* may show all gradations between the normal basin-shaped chloroplast with a lateral pyrenoid, and one with massive lateral thickenings which can touch or fuse with one another to form a bridge containing the pyrenoid as in *Agloë* (Gerloff, 1940, *C. humiphilos*, text-fig. 28). This may go a stage further, when more than two lateral lobes fuse centrally to form a more or less markedly stellate chloroplast (*C. varians* n.sp., Fig. 2 D-H; *C. astigmata* n.sp., Fig. 2 I-K; *C. stellata* Dill, Gerloff, 1940, text-fig. 25, Figs. 10, 11). Gerloff did not study any markedly stellate species. Similarly, the basal thickening in the subgenus *Euchlamydomonas* is very variable (*C. Muriella* forma A, Fig. 2 S-V) and may be absent (*C. Snowiae* var. *palmelloides* n.var., Fig. 1 L; *C. mutabilis* Gerloff, 1940, text-fig. 42, p. 399).

(7) The presence or absence of pyrenoids is constant. When present, the position of the pyrenoid varies according to the position of the thickened portions of the chloroplast (Gerloff, 1940, text-fig. 35, p. 379). Even as the chloroplast form is the same in the majority of the cells of a population, so does the pyrenoid lie in the same position. Two (or more) pyrenoids commonly occur in some cells in a species usually having only one (*C. humiphilos* Gerloff, 1940, pp. 358-62; *C. Snowiae* var. *palmelloides*, Fig. 1 K).

C. THE SPECIES

Gerloff (1940) has tabulated and given a key to some 300 species and states that many new species are to be found in the soil, several of which he describes. Fritsch & John (1942) likewise found several species in soil. In some cases, species found in cultures may not be true soil algae since they occur with well-known aquatic Volvocales (e.g. *Pandorina* and *Eudorina*; cf. Jacobsen, 1910; Moewus, 1935). In the present investigation, species were found by direct observation on twenty-three soils, but none occurred with regularity on any particular type.

All the species possess two contractile vacuoles. A peculiar feature is the absence of a stigma in several.

(1) *C. pseudo-elegans* Fritsch & John (1942, p. 373) var. *minor* n.var., Fig. 1 A.

The ovate-oblong cells ($12-14\mu$ l., 7μ br.) have a prominent rounded papilla, thin wall and small stigma lying in the anterior half of the cell. The flagella are longer than the cell (c. 16μ). The nucleus is anterior. The parietal chloroplast is thickened on the side in which the pyrenoid lies. On one soil (S38; for list of soils see Lund, 1946, pp. 106-7).

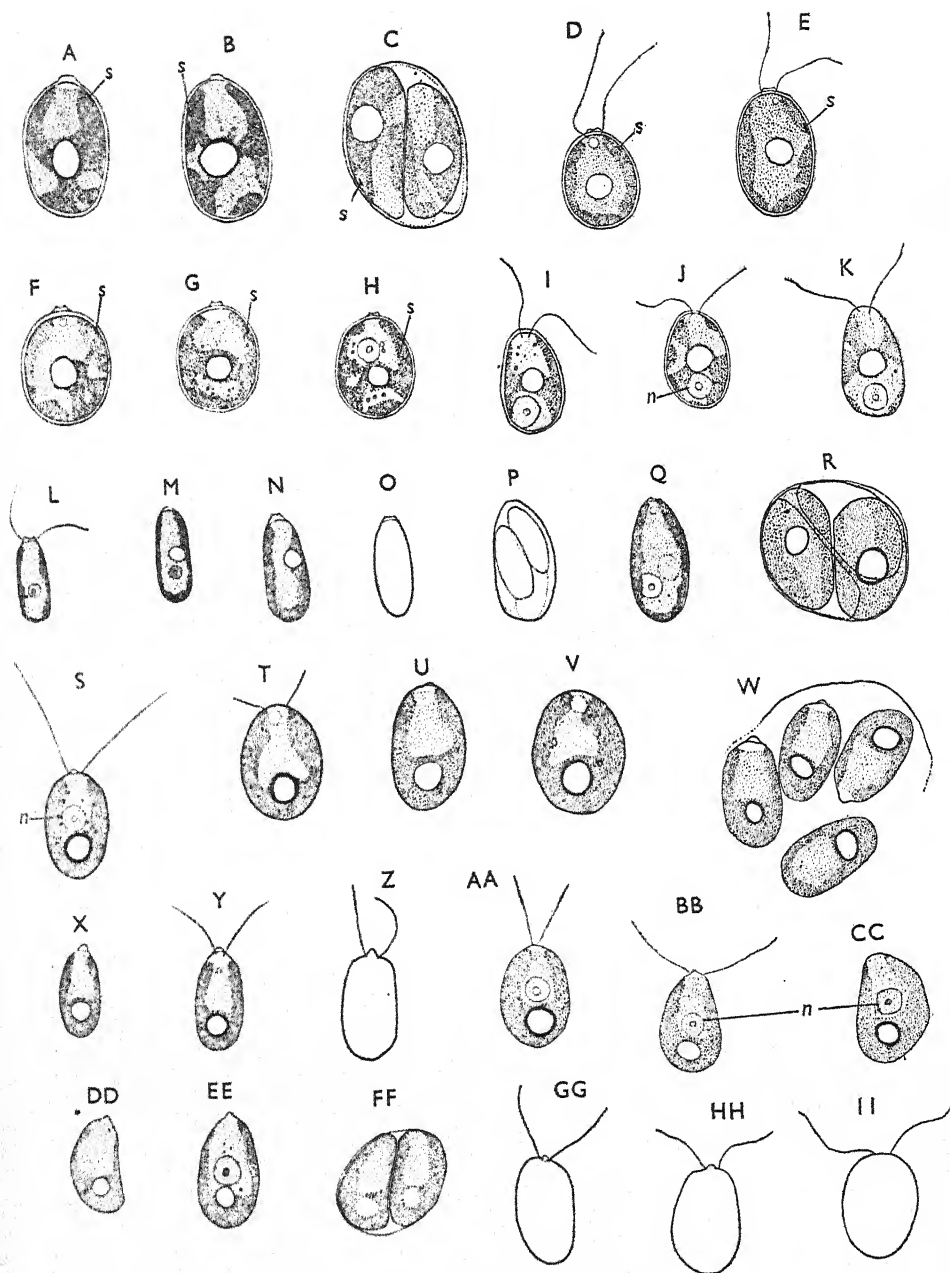


Fig. 2. A-C, *Chlamydomonas macroplastida* n.sp. forma; D-H, *C. varians* n.sp.; I-K, *C. astigmata* n.sp.; L-Q, *C. oblongella* n.sp.; R-II, *C. Muriella* n.sp.; R-V, forma A; W-Z, forma B; AA-II, forma C; C, P, Q, R, T-W, CC, FF, non-motile and division stages; O, P, Z, GG, HH, II, stained in fuchsin and gentian violet. A-C, I-II, $\times 1000$; D-H, $\times 1500$.

The type differs in the larger cells which may be slightly curved or have one face more flattened than the other, while the stigma is streak-like and the papilla smaller.

(2) *C. Snowiae* Printz. (*C. pluristigma* Bristol pro parte), Fig. 1 B-H.

The motile cells ($11-13\ \mu$ l., $7.5-10\ \mu$ br.) are oval to oblong with a delicate papilla not clearly delimited from the cell wall. The stigma is anterior and small. The basically cup-shaped chloroplast covers most of the inner surface of the wall and has several cushion-shaped thickenings. In some cells (Fig. 1 B) it appears that fusion of two of the latter has occurred, for the central pyrenoid lies in a chloroplast bridge. These often lack a papilla and are larger and more oval than the motile cells (to $15\ \mu$ l. and $13\ \mu$ br.). The stigma is no longer visible but contractile vacuoles are retained. The chloroplast is joined to the central pyrenoid by two to five lobes so that a stellate condition ensues (Fig. 1, F-H). There is an alternation between motile and non-motile states. The motile cells soon come to rest. From hanging-drop cultures, it appears that 24 hr. is the maximum period of motility. Usually it is shorter. On a moist substratum, the non-motile cells enlarge and become more and more ovoid till division occurs into four daughter cells. Immersion in water leads to the emergence of these cells to initiate a new motile stage.

This species clearly belongs to the *C. pluristigma* of Bristol (1920; cf. James, 1935, only known from Britain) in the type of chloroplast, central pyrenoid, small stigma and faintly delimited papilla. The cells are smaller than those of Bristol and considerably more so than those of James ($17-24\ \mu$ l., $9-18\ \mu$ br.) while the accessory stigmata described by Bristol were never seen. James only found these in a few specimens. Gerloff (1940, p. 412) finds that *C. Snowiae* Printz shows variation in its chloroplast structure which joins it to *C. pluristigma* Bristol. The latter he considers to be a variety (var. *pluristigma* Gerloff) with accessory stigmata. Gerloff, Bristol and James do not record the non-motile cells with more or less marked stellate chloroplasts.

Known from British, European and American (Smith, 1946) soils. Present on nine soils.

Var. *palmelloides* n.var. Fig. 1 I-N.

The cells ($9-13\ \mu$ l., $5-8\ \mu$ br.) are ovoid with a pointed anterior and rounded posterior end. The wall is thin. The chloroplast is similar to that of the species though the pyrenoid is less frequently in a central bridge. Two pyrenoids are occasionally present (Fig. 1 K). As in the species, the motile state rarely lasts longer than 24 hr. but the non-motile cells form a well-marked palmelloid growth, division only being seen in this stage.

Common over most of the year in one soil (S3).

(3) *C. tetras* n.sp., Fig. 1 O-U.

This species is characterized by the well-marked non-motile stage. Observations in a moist chamber showed that this stage regularly alternates with the motile one and predominates when the moisture content of the soil is low.

The non-motile cells ($6-7\ \mu$ l., $5-7\ \mu$ br.) possess a basin-shaped parietal chloroplast with a thickened basal portion containing the pyrenoid. The cells are commonly in pairs or tetrads (Fig. 1 P). No mucilage is produced. The motile stage is usually initiated by transferring these cells from agar or soil into water. The motile cells ($6-7\ \mu$ l., $3.5-4\ \mu$ br.) are oblong-elliptic and resemble those of *C. terrestris* Boye Pet. (Petersen, 1932, pp. 28-9) apart from the usually basin-shaped chloroplast. The lateral pyrenoid lies midway along the margin of the cell, usually in a thickened part of the chloroplast. There is a small

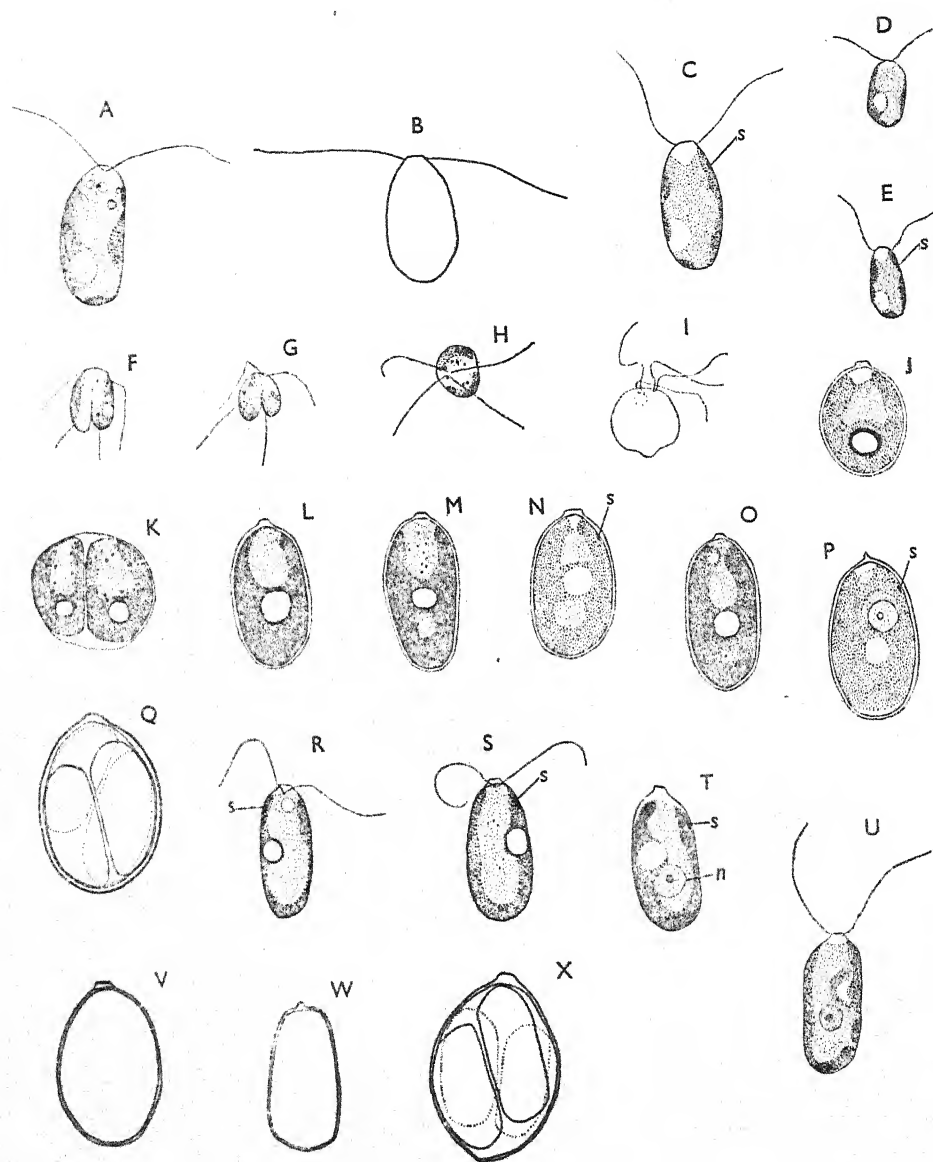


Fig. 3. A-I, *Chlamydomonas planoconvexa* n.sp.; J, K, *C. Britannica* n.sp.; L-Q, *C. macroplastida* n.sp.; R-S, V-X, *C. Moewusii* Gerloff var. *major* n.var.; T, U, *C. Moewusii* Gerloff forma *microstigmata* n.f.; K, Q, X, division stages; F-I, conjugation; B, I, V, W, stained in fuchsin and gentian violet. A-C, $\times 1750$; rest, $\times 1000$.

elongate anterior stigma and the two flagella are as long as or slightly longer than the cell. There is no papilla. After the short period of motility, the cells come to rest, lose their flagella and round off (Fig. 1 S) prior to resuming division into the pairs and tetrads. From two soils (S2, 11).

It differs from *C. terrestris* Boye Pet. (1932) in the absence of mucilage surrounding the non-motile cells; the presence of a stigma and, judging from Petersen's Fig. 10a, the more or less cup-shaped chloroplast in the motile stage. Petersen's doubts as to whether *C. terrestris* is really a *Chlamydomonas* apply equally to my species. The presence of more or less prolonged non-motile stages is, however, not uncommon in soil Chlamydomonads and seems to depend generally on the presence or absence of free water (cf. *C. pseudogloeogama* Fritsch & John, 1942, p. 373).

(4) *C. pyramidalis* n.sp., Fig. 1 V, W.

In the plane of the flagella (Fig. 1 V) the cell ($17.5\text{--}20\ \mu\text{ l.}$, $7.5\text{--}9\ \mu\text{ br.}$) is oblong, with parallel margins and widely rounded extremities. In the opposing plane one side is flattened and the other convex. There is a well-marked pyramidal papilla with the two flagella emerging close to its base. The flagella are approximately the length of the cell. The parietal chloroplast is basin-shaped with a thicker band half girdling the cell in the middle (Fig. 1 W). The single pyrenoid lies in this band. In small numbers on one soil (S38).

It shows some similarity to *C. agloiformis* Pascher (1927, p. 252), but the latter has a very large stigma, small papilla and cylindrical chloroplast with a central bridge.

(5) *C. macrostellata* n.sp., Figs. 1 X-Z, 2 A-C.

The ovate-oblong cells ($14\text{--}19\ \mu\text{ l.}$, $8\text{--}12\ \mu\text{ br.}$) have a papilla which appears flat-topped in the plane of the flagella and round in the opposing plane. There is a streak-like stigma which is often difficult to observe and sometimes invisible. The nucleus is anterior. The flagella are cell length. The chloroplast is massive and stellate with a central pyrenoid which may be very large (Fig. 1 Z). The arms of the chloroplast flatten out at the periphery of the cell. In a form from one soil (S28, Fig. 2 A-C) the number of arms are only three to four and the stigma is rather shorter than in specimens from the other four soils (S12, 16, 19, 49). Division into four (Fig. 2 C).

(6) *C. varians* n.sp., Fig. 2 D-H.

The cells ($11\text{--}13\ \mu\text{ l.}$, $8\text{--}10\ \mu\text{ br.}$) are usually subspherical to oval but sometimes ovate-oblong (Fig. 2 E). The delicate papilla, only seen clearly in stained specimens and more evident in young than in old cells, has a central U-shaped depression. The stigma is streak-like and, like the nucleus, anterior. The parietal chloroplast covers most of the wall. Its margins are often lobed, and one or more of these lobes may reach the central pyrenoid so that it lies in a chloroplast bridge (Fig. 2 G) or is joined to one side of the chloroplast only (Fig. 2 F). Occasionally a somewhat stellate condition is reached (Fig. 2 H). Division into eight. On one soil (S33).

(7) *C. astigmata* n.sp., Fig. 2 I-K.

The ovoid or widely pyriform cells ($11\text{--}15\ \mu\text{ l.}$, $5\text{--}9\ \mu\text{ br.}$) possess no papilla or stigma. The nucleus is posterior. The flagella are about the length of the cell or slightly shorter.

The chloroplast covers most of the inner margin of the wall and shows internal thickenings. It is joined to the central pyrenoid either by a bridge or by three arms so that, as in the preceding species, it may be somewhat stellate.

Division into eight. On one soil (S38).

(8) *C. oblongella* n.sp., Fig. 2 L-Q.

The cells ($11-16\mu$ l., $4-8\mu$ br.) are oblong with parallel margins when young. Older larger cells, especially when about to divide, may have one or both margins slightly convex (Fig. 2 P, Q), while cells of intermediate size are often slightly wider at the base than at the apex. The delicate papilla has a shallow central U-shaped depression. There is no stigma and the nucleus is posterior. The parietal cup-shaped chloroplast has a lateral pyrenoid. Division into four. On one soil (S39).

(9) *C. Muriella** n.sp., Fig. 2 R-II.

The three following show intermediate stages and appear to be forms of one species.

Forma A, Fig. 2 R-V. The cells ($12.5-18\mu$ l., $9-13\mu$ br.) are elongate ovoid when motile and widely ovoid to oval when non-motile. The latter state is probably generally antecedent to division. No papilla is visible in unstained cells. After staining, a small delicate papilla is visible in the motile cells but not in the non-motile cells (Fig. 2 T-V). The chloroplast is cup-shaped and the pyrenoid lies in the basal thickening. No stigma. Nucleus approximately central. Division into four (Fig. 2 R).

It differs from the following in the wider, more ovoid cells and very delicate papilla. From one soil (S3).

Forma B, Fig. 2 W-Z. The cells ($11-15\mu$ l., $6-8\mu$ br.) are ovate-oblong with a prominent rounded knob-shaped papilla. No stigma. Flagella about three-quarters the length of the cell. Chloroplast cup-shaped with a pyrenoid in the basal thickening. Division into four (Fig. 2 W). From one soil (S30).

Forma C, Fig. 2 AA-II. The cells ($14-15\mu$ l., $6-11\mu$ br.), when young, are commonly ovoid to pyriform-ovoid in one view and asymmetric in the other (Fig. 2 BB-DD), one margin being convex and the other being plane or concave. The larger, older cells are ovoid to oval (Fig. 2 HH-II). The difference in shape may be related to the asexual reproduction. The characteristic asymmetry of the young cells is due to mutual pressure of the daughter cells within the mother cell wall (Fig. 2 FF). There is a small rounded papilla in younger cells. This is very indistinct in living cells and, in the larger cells, is often absent. Other features as in formae A and B.

From one soil (S30).

In chloroplast structure, position of pyrenoid and nucleus, papilla and absence of stigma, it resembles *C. Franki* Pascher (1927, p. 222), of which these may be forms. The flagella of *C. Franki*, however, judging from the figures, are extraordinarily thick, while the papilla, which is retained even in non-motile cells, is even more prominent than in forma B. *C. Debaryana* Goroschankin (Gerloff, 1940) possesses a stigma and a usually prominent papilla which differs in shape in the two planes.

(10) *C. planoconvexa* n.sp., Fig. 3 A-I.

The cells ($9-11\mu$ l., $5-8\mu$ br.) are ovoid to oblong in one plane (Fig. 3 C), but in the opposing (flagella) plane usually have one side flattened or even weakly concave and the

* Named after B. Muriel Bristol Roach.

other convex (Fig. 3 A). The anterior end is flattened but hardly delimited as a definite papilla even in large cells. In the young cells this anterior flattening is only clearly seen after staining. Flagella about one and a half times as long as the cell. The thin streak-like stigma is anterior and closely opposed to the cell wall. It is commonly indistinct or invisible. Chloroplast parietal with irregular internal thickenings. Pyrenoid lateral, lying in one of the more basal thickenings (Fig. 3 A, D).

Asexual division into four, eight or sixteen cells. Sexual reproduction occurred in a moist culture on the days immediately succeeding collection. The gametes ($6-9\mu$ l., $2.5-3\mu$ br.) are anisogamous, though the size difference is often very small. The chloroplast is lateral and a pyrenoid is sometimes visible. There is a stigma similar to that of the vegetative cells.

From one soil (S40).

(11) *C. macroplastida* n.sp., Fig. 3 L-Q.

The cells ($17-25\mu$ l., $8-17\mu$ br.) are oblong to nearly oval. The papilla is ridge-shaped, being flat-topped in one view and bluntly pointed in the other. Very rarely it is slightly to one side of the cell apex. Cell wall thick. Stigma minute, about twice as long as broad; often invisible. Nucleus anterior. Chloroplast massive, cup-shaped, with a large basal thickening reaching halfway or more up the cell and containing the pyrenoid. Sometimes there is a break in the continuity of the basal thickening below the pyrenoid so that it appears to lie in a bridge (Fig. 3 M-O).

Division into two or four. From eight soils.

C. angulosa Dill (Pascher, 1927, p. 232) shows some resemblance in chloroplast and papilla, but the pyrenoid is markedly rectangular and the stigma is much larger. Gerloff (1940) has shown that the shape of the pyrenoid may vary from spherical to somewhat angular but never to the extent characteristic of *C. angulosa*.

(12) *C. Britannica* n.sp., Fig. 3 J-K.

The cells ($12-16\mu$ l., $8-19\mu$ br.) are oval to subspherical. The papilla is ridge-shaped as in the preceding species. No stigma. Nucleus approximately central. There is a single pyrenoid in the large basal thickening of the cup-shaped chloroplast.

Division into two or four. On four soils.

It differs from *C. proboscigera* Korsch. (Pascher, 1927, p. 216) in the absence of a stigma. The papilla of that species appears to be flat-topped in both views (Pascher, 1927, p. 216).

(13) *C. Moewusii* Gerloff (1940) var. *major* n.var., Fig. 3 R, S, V-X.

The cells ($16-24\mu$ l., $6-14\mu$ br.) are oblong or ovoid-oblong when young, but older cells, which may be non-motile, and probably are a stage prior to division, become more ovoid. There is a small wedge-shaped papilla, flat-topped in one view and bluntly pointed in the other. Flagella the length of the cell or somewhat shorter. Stigma large, anterior and appressed to the wall. Nucleus posterior. Chloroplast cup-shaped, with the lateral pyrenoid lying in a small median bulge. Its internal outline is more regular than in the species (Gerloff, 1940). Division into four. On one soil (S35). Though larger and relatively narrower than *C. Moewusii* Gerloff ($9-15\mu$ l., $5.4-8\mu$ br.) the cells show a close similarity to those grown in Benecke solution (Gerloff, 1940, p. 332, text-fig. 5, Figs. 15, 16).

Forma *microstigmata* n.f., Fig. 3 T, U, differs in the small streak-like stigma. Non-motile cells and reproduction not seen. It is possible that this should be included in the species (cf. Gerloff, 1940, pp. 321-2 and text-fig. 1).

C. gloeogama Korsch. var. *Hartmanni* (Moewus) Gerloff nov. comb (Gerloff, 1940).

My thanks are due to Prof. F. E. Fritsch for advice and criticism and to Prof. J. M. Webster in whose laboratory most of the work was carried out.

SUMMARY

Chlamydomonas spp. are common in soil. Ten new species are described with observations on specific delimitation in the genus.

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VARIATION IN THE SIZE AND SHAPE OF SPORES, BASIDIA AND CYSTIDIA IN BASIDIOMYCETES

By E. J. H. CORNER, M.A., F.L.S.

(With 4 figures and 14 graphs in the text)

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INTRODUCTION

The rudiments of basidiospores are generally subglobose. Either they remain so by swelling outward from the tip of the sterigma, or, more commonly, they become ellipsoid in a direction practically parallel with the long axis of the basidium. In many species with ellipsoid spores there is a great range in length of the mature spores but comparatively little in width. Such spores continually change shape as they grow, becoming more and more elongate; and one would expect, therefore, that closely related species, differing mainly in spore size, should have differently shaped spores. The tendency is to classify species according to the shape of the spore and to separate species according to its size. The method seems unnatural and, as it may seriously affect systematy, I have studied the problem in groups of very closely related species. The initial difficulty has been to discover such groups because local floras do not necessarily contain very closely related species. Thus, *Amanita muscaria* and *A. rubescens*, *Paxillus involutus* and *P. atrotomentosus*, or *Clavaria argillacea* and *C. vermicularis* are not very closely related, for each has much closer tropical allies. For the purpose of discovering affinities and, so, of arriving at truly mycological comparisons, I have monographed the species of *Clavaria* and allied genera. The results suggest a fundamental law of hyphal growth, and I have accordingly abstracted a few illustrations and added some examples from other groups in order to give a general account.

MATURE SPORES

Method. I have measured spores from fresh spore-prints and grouped the sizes according to differences in length. The measurements were made with an eyepiece micrometer and an oil-immersion objective. I have mostly used differences in length of 0.5μ and have always omitted the apiculus, as in Fig. 1a. I refer to the length as *D* and the width

as d . Whenever possible, I have measured twenty spores for each value of D , but ten spores are probably enough for most purposes. In that the first spores to be seen in the appropriate position are measured the sampling is random, but it is always necessary to search for spores at the upper and lower limits of D , and one will be lucky to find more than one or two examples in the course of an hour. I arrange the measurements by increasing values of D and, when D is the same, then by increasing values of d . I then average the data for convenient ranges of D , as in Tables 1, 2 and 8. The average data from the tabular analysis I call the *working data* for the graphical analysis.

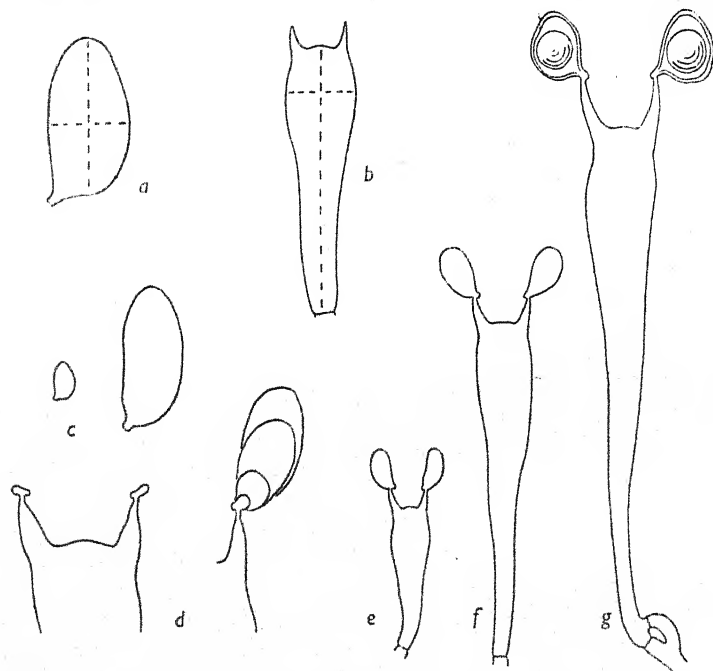


Fig. 1. Diagrammatic sections of a spore (a) and a basidium (b) to show the measures of length and width; c, micro- and macrospores of *Hygrophorus firmus*, $\times 800$; d, developing macrospores of *H. firmus*, $\times 800$; e, f, g, basidia of *Clavaria* sp., *C. vermicularis* and *C. fusiformis* respectively, $\times 1000$.

The working data consist of D , d and E , which is the ratio of $D : d$ and expresses, conveniently, the shape or elongation of the spore (in the common, but not mathematical, sense of ellipticity). Thus if E is unity, the spore is globose and, as E increases, the spore elongates parallel with the long axis of the basidium; only in very young spores is E less than unity, as in Figs. 1 d and 3 h. This ratio proved to be a short cut to the discovery that the graph relating E and D for any one species can be idealized as a straight line. Such a graph I call a *sporograph* because a name is needed for this analytical method of studying basidiospores. The locus of the working data I call the species-locus or, if idealized, the *species-line*.

I have averaged the measurements for several reasons. Personal errors in measurement are unavoidable with such minute objects. The spores are not exactly elliptic in optical section but always flattened slightly on the adaxial side, that is, the side toward the long axis of the basidium. The width in the sagittal plane, which is the one that I have taken as

being most easily identified, may be appreciably less ($0.5-1\mu$ or more) than in the tangential plane at right angles, and it is often difficult to be sure that the spore lies exactly in the sagittal plane. There is also a normal fluctuation in d for a given value of D . The sporograph should, therefore, show a species-band (as in Graph 1) rather than a species-line, but the determination of the limits of a band requires many more data than that for its direction, which is all that initial analysis requires. Actually, the species-locus sharpens investigation by making one inquire into the reasons for this fluctuation and for certain deviations which often lead to a fall or rise of the locus at its upper limits. These problems must be left until the basidium unit as a whole can be considered in the detail of its mechanism and geometry.

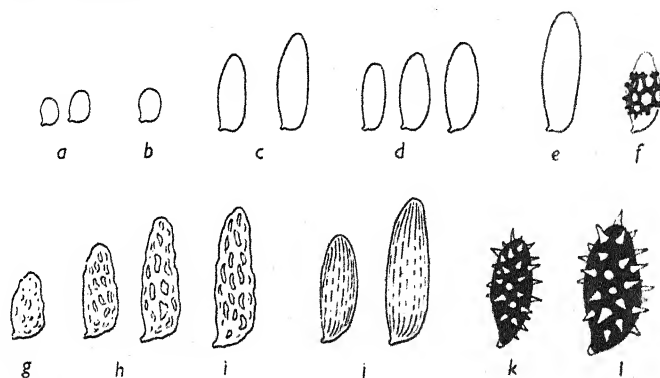


Fig. 2. Spores of *Boletus* and *Clavaria*, mentioned in the text. a, *Boletus* '64'; b, *Boletus* '8'; c, *B. funerarius*; d, *Boletus* '42 f'; e, *Boletus* '62'; f, *Boletus* '19 b', with brown reticulum partly covering the spore; $\times 800$. g, *Clavaria subgelatinosa*; h, *C. formosa* (two spores); i, *C. flava*; j, *C. botrytis*; k, *C. fragillima*; l, *C. cyanocephala* (*C. fragillima* and *C. cyanocephala* with brown spore-wall and hyaline spines); $\times 1000$.

Another datum is the *species-point*. Spore size is given in descriptions as D to $D' \times d$ to d' , to cover the commonly observed range of D and d . Construction of sporographs is arduous and so to use the many accurate spore measurements which have been published in the last twenty or thirty years, I take the mean values of D and d to give a mean value for E . From many tests, which I need not detail, I have found that the mean values are very near the average, provided that the extremes have been fairly estimated; indeed, in five minutes one can obtain by inspection of a slide extremes which will give a mean value of E differing only in the second decimal place from an average obtained after several hours of exacting measurement and tedious arithmetic; one need not fear taking the very shortest, longest, fattest and leanest spores as the most abnormal, for they will usually give the best mean values, e.g. *Boletus funerarius* with spores $10-14.7 \times 5-6.5\mu$, the mean values $12.35 \times 5.75\mu$ ($E=2.15$), were obtained in a few minutes and agree almost exactly with the average of 218 spores, $12.35 \times 5.71\mu$ ($E=2.16$), obtained after nearly five hours' work. Undoubtedly, the future will slowly supply sporographs for all species; in the meantime, species-points can be used for comparison with the few available sporographs and to direct inquiry into the more interesting fields. In the graphs I have shown species-points as triangles in contrast with the circles of average-points.

To specify a locus, I use the notation $D : E-D' : E'$, for instance $0 : 1.48-15.0 : 2.31$ for *Boletus funerarius*. The notation enables one to rule a line quickly for reference when details are not needed.

Clavaria formosa. This is one of the earlier species which I studied. My results can well be improved, as I have learnt from further experience, e.g. the species of *Boletus* to be mentioned presently, but *Clavaria formosa* is a very widespread, well-known and readily identified fungus for which there is much information, and it illustrates the features of the

Table 1. *Sporograph data for two fruit-bodies of Clavaria formosa; individual spore measurements*

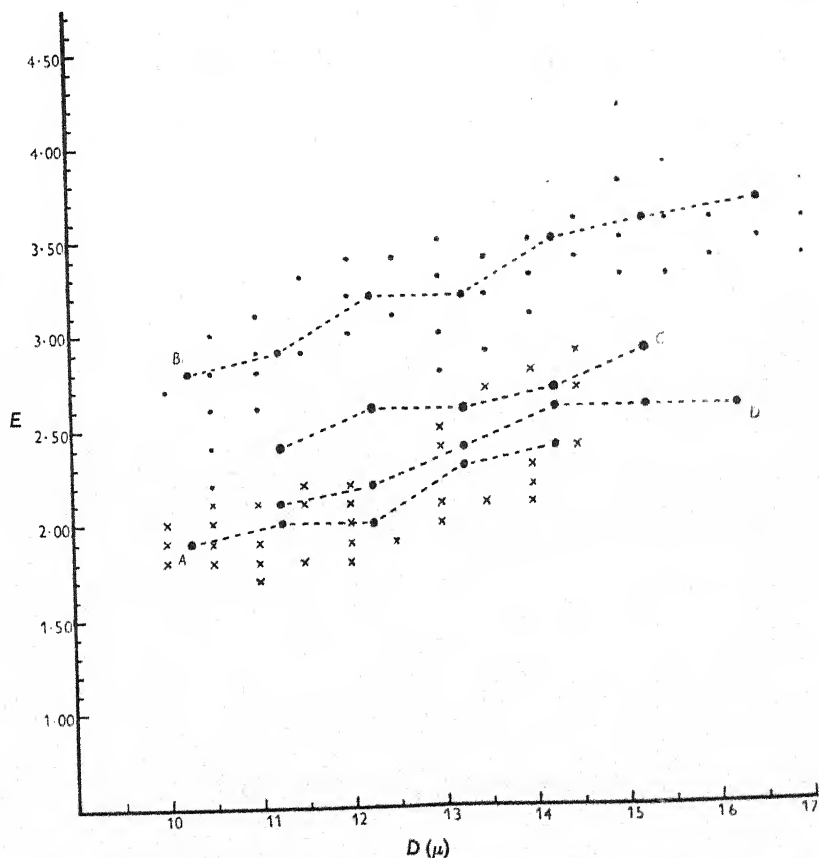
Fruit-body A, from Austria			Fruit-body B, from England		
Spore size in μ	E	No. of records	Spore size in μ	E	No. of records
10 \times 5.0	2.0	1	10 \times 3.7	2.7	2
10 \times 5.3	1.9	2	10.5 \times 3.5	3.0	1
10 \times 5.5	1.8	1	10.5 \times 3.7	2.8	2
10.5 \times 5.0	2.1	1	10.5 \times 4.0	2.6	2
10.5 \times 5.3	2.0	1	10.5 \times 4.3	2.4	2
10.5 \times 5.5	1.9	2	10.5 \times 4.7	2.2	1
10.5 \times 5.7	1.8	2	11 \times 3.5	3.1	2
11 \times 5.3	2.1	2	11 \times 3.7	2.9	4
11 \times 5.7	1.9	1	11 \times 4.0	2.8	1
11 \times 6.0	1.8	2	11 \times 4.3	2.6	1
11 \times 6.3	1.7	1	11.5 \times 3.5	3.3	1
11.5 \times 5.3	2.2	2	11.5 \times 4.0	2.9	1
11.5 \times 5.5	2.1	1	12 \times 3.5	3.4	4
11.5 \times 6.5	1.8	1	12 \times 3.7	3.2	1
12 \times 5.5	2.2	2	12 \times 4.0	3.0	3
12 \times 5.7	2.1	1	12.5 \times 3.7	3.4	1
12 \times 6.0	2.0	1	12.5 \times 4.0	3.1	1
12 \times 6.3	1.9	3	13 \times 3.7	3.5	1
12 \times 6.5	1.8	2	13 \times 4.0	3.3	3
12.5 \times 6.5	1.9	1	13 \times 4.3	3.0	1
13 \times 5.3	2.5	2	13 \times 4.7	2.8	1
13 \times 5.5	2.4	1	13.5 \times 4.0	3.4	1
13 \times 6.3	2.1	2	13.5 \times 4.3	3.2	1
13 \times 6.5	2.0	2	13.5 \times 4.7	2.9	2
13.5 \times 5.0	2.7	2	14 \times 4.0	3.5	3
13.5 \times 6.3	2.1	1	14 \times 4.3	3.3	1
14 \times 5.0	2.8	1	14 \times 4.5	3.1	1
14 \times 6.0	2.3	3	14.5 \times 4.0	3.6	4
14 \times 6.3	2.2	2	14.5 \times 4.3	3.4	1
14 \times 6.7	2.1	1	15 \times 3.5	4.2	1
14.5 \times 5.0	2.9	1	15 \times 4.0	3.8	2
14.5 \times 5.3	2.7	1	15 \times 4.3	3.5	1
14.5 \times 6.0	2.4	1	15 \times 4.5	3.3	3
			15.5 \times 4.0	3.9	1
			15.5 \times 4.3	3.6	1
			15.5 \times 4.7	3.3	1
			16 \times 3.5	4.6	1
			16 \times 4.5	3.6	1
			16 \times 4.7	3.4	3
			16.5 \times 4.7	3.5	1
			17 \times 4.5	3.8	1
			17 \times 4.7	3.6	2
			17 \times 5.0	3.4	1

sporograph better than any other that I have analysed. The working data for four fruit-bodies and the details for two of them are shown in Tables 1 and 2; their analysis is shown in Graphs 1 and 2.

Graph 2 gives the species-locus derived from the average of the four fruit-bodies and also a species-point-locus derived from the mean data of my own and of other authors, as given in Table 3. These data can be grouped into three sets according to *D*; there are

Table 2. *Sporograph-data for Clavaria formosa; averages from four fruit-bodies of different collections*

Fruit-body	Range of spore size ($D \times d$) in μ	Range in D (μ)	Averages for ranges in D			
			D (μ)	d (μ)	E	No. of spores
A (Austria)	10.0-14.5 \times 5.0-6.7	10.0-10.5	10.25	5.4	1.9	10
		11.0-11.5	11.25	5.6	2.0	10
		12.0-12.5	12.25	6.1	2.0	10
		13.0-13.5	13.25	5.8	2.3	10
		14.0-14.5	14.25	5.9	2.4	10
B (England)	10.0-17.0 \times 3.5-5.0	10.0-10.5	10.25	3.7	2.8	10
		11.0-11.5	11.25	3.9	2.9	10
		12.0-12.5	12.25	3.8	3.2	10
		13.0-13.5	13.25	4.1	3.2	10
		14.0-14.5	14.25	4.1	3.5	10
		15.0-15.5	15.25	4.2	3.6	10
		16.0-17.0	16.50	4.5	3.7	10
		11.0-11.5	11.25	4.7	2.4	10
C (England)	11.0-15.5 \times 4.0-6.0	12.0-12.5	12.25	4.7	2.6	10
		13.0-13.5	13.25	5.1	2.6	10
		14.0-14.5	14.25	5.3	2.7	10
		15.0-15.5	15.25	5.3	2.9	10
		16.0-17.0	16.50	5.4	2.1	10
D (England)	11.0-17.0 \times 5.0-7.0	11.0-11.5	11.25	5.6	2.2	10
		12.0-12.5	12.25	5.5	2.4	10
		13.0-13.5	13.25	5.5	2.6	10
		14.0-14.5	14.25	5.5	2.6	10
		15.0-15.5	15.25	5.9	2.6	10



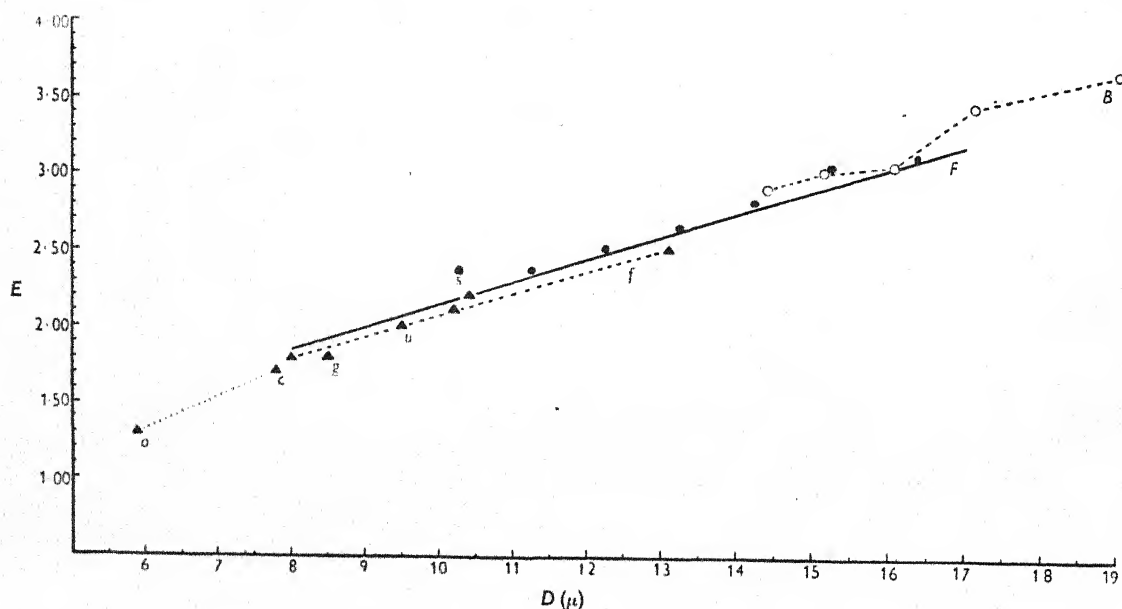
Graph 1. Sporograph for *Clavaria formosa*, showing the actual data for two fruit-bodies (as in Table 1; fruit-body A as dots, fruit-body B as crosses), and the average points for four fruit-bodies (as in Table 2). D is the spore-length and E is the ratio of spore-length to width.

Table 3. *Sporograph data for Clavaria formosa and related species*

Species	Range of spore size ($D \times d$) in μ	Range of D (μ)	Averages for ranges of D			
			D (μ)	d (μ)	E	No. of records
<i>C. formosa</i>	10.0-17.0 \times 3.5-7.0 (See Table 2)	10.0-10.5	10.25	4.36	2.35	20
		11.0-11.5	11.25	4.79	2.35	40
		12.0-12.5	12.25	4.90	2.50	40
		13.0-13.5	13.25	5.04	2.63	40
		14.0-14.5	14.25	5.09	2.80	40
		15.0-15.5	15.25	5.03	3.03	30
		16.0-17.0	16.35	5.19	3.15	20
	Mean values	—	13.1	5.2	2.52	Corner
	8-13 \times 3.5-6	—	10.2	4.9	2.1	Auctt.* (35)
	7-9 \times 3.5-5.5	—	8.0	4.5	1.8	Auctt.† (4)
<i>C. conjunctipes</i>	7-10 \times 4-5	—	7.8	4.5	1.7	Coker* (5)
var. <i>odora</i>	5.5-6.3 \times 4-4.8	—	5.9	4.4	1.3	Coker* (1)
<i>C. gelatinosa</i>	7.5-10 \times 4.5-6	—	8.5	4.7	1.8	Coker* (3)
<i>C. secunda</i>	8-12.5 \times 4-5.5	—	10.4	4.7	2.2	Coker* (7)
<i>C. subgelatinosa</i>	8.5-10.5 \times 4.5-5	—	9.5	4.8	2.0	Corner* (1)

* Averages of the mean values of spore records published by various authors, the number of records given in brackets.

† Average of four records of unusually short spores.



Graph 2. Sporograph for *Clavaria formosa* and closely allied species (as in Table 3). *F*, the species-line for *C. formosa*, derived from the average data of the four fruit-bodies (Table 2), shown as black circles, and from the three species-points (Table 3) joined by the broken line *f*; *c*, the point for *C. conjunctipes*; *g*, the point for *C. gelatinosa*; *o*, the point for *C. conjunctipes* var. *odora*; *s*, the point for *C. secunda*; *u*, the point for *C. subgelatinosa*. *B*, the sporograph-points of *C. botrytis* (Table 4), as white circles. (In this and the following graphs, average points are shown as circles and species-points as triangles.)

spores *c.* 13μ long (my data), spores *c.* 10μ long (thirty-five sets of data from other authors) and spores *c.* 8μ long (unusually short spores mentioned by Coker). The three points lie practically in a straight line which is almost parallel with the average species-locus and just below it. The range in the mean value of *D* is 5μ ($8\text{--}13\mu$), but that for *d* is only 0.7μ ($4.5\text{--}5.2\mu$); for the average species-locus the ranges are 10μ for *D* and 3.5μ for *d*. The sporograph shows that this remarkably simple relation between the length and width of the spore illustrates a general control of its growth by some fundamental law. An average point for the whole range of *D* and *d*, as is often given now in mycological descriptions, would be a meaningless simplification. The sporograph shows that the supposedly aberrant very long and very short spores are extremes of a general rule and, therefore, not to be neglected; a locus, not a point, is the desideratum in the study of the size and shape of basidiospores.

There are four species very closely allied with *C. formosa* as given in Table 3. The species-point of *C. secunda* (North America) lies near the middle of the locus for the palaearctic *C. formosa*; *C. secunda* appears as a pink form of *C. formosa*. The species-points for *C. gelatinosa* (North America) and *C. subgelatinosa* (Malaya) lie near the beginning of the *formosa*-locus and may well coincide; their fruit-bodies appear as progressively gelatinous modifications of *C. formosa* and could not be distinguished by spore-characters. The species-point-locus for *C. conjunctipes* (North-America) and its variety *odora* suggest the extension of the *formosa*-locus toward the origin and to the subglobose shape; the fruit-bodies of *C. conjunctipes* appear as reduced and simplified states of *C. formosa*. I conclude that these very closely allied species have the same kind of spore, conforming to the same locus on the sporograph and differing principally in size. Thus the 5.5μ subglobose spore of *C. conjunctipes* var. *odora* is related with the $10\text{--}17\mu$ cylindric-fusiform spore of *C. formosa*.

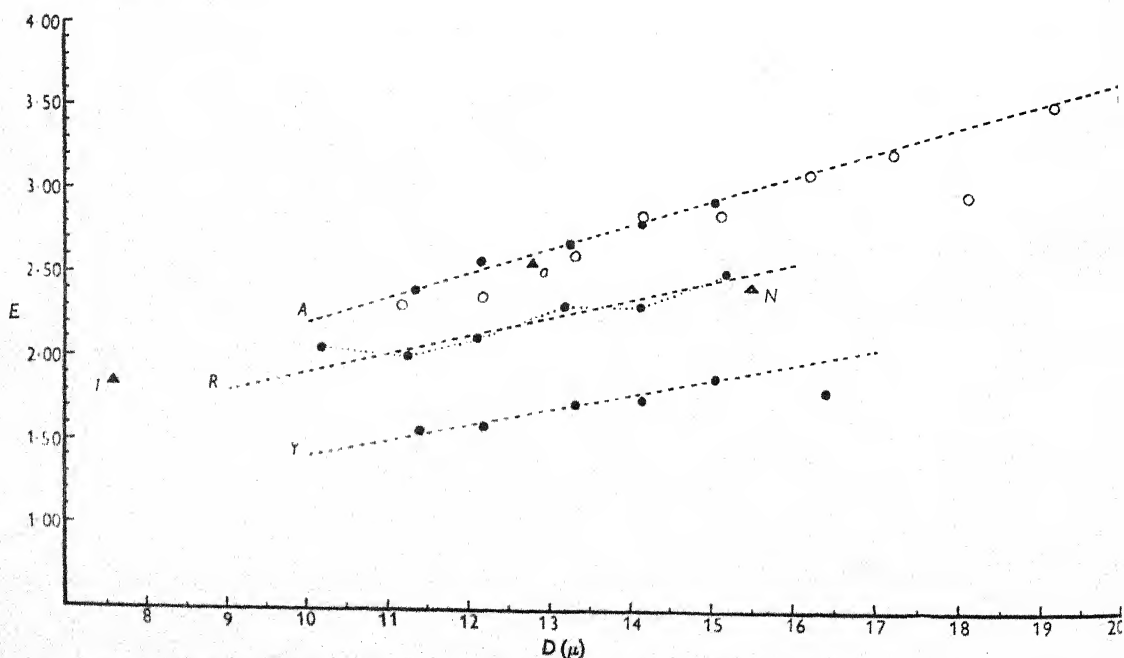
Clavaria aurea, *C. flava*, *C. botrytis*, *C. fragillima* and *C. cyanocephala* (Table 4, Graphs 2 and 3). These species are related with *C. formosa*. The first two have spores very like those of *C. formosa*, from which they differ mainly in the yellow colour of the fruit-body; yet there are a sufficient number of species with this peculiarity to make it convenient to speak of a 'Flava-group' as well as a 'Formosa-group'. The locus of *C. aurea* on the sporograph (the broken line *A* in Graph 3) practically coincides with the *formosa*-locus, and the points of *C. flava*, which has more variable spores, clearly conform; certainly, my data reveal no significant difference. *C. botrytis* has fruit-bodies resembling those of *C. aurea* but with the pink colour of *C. formosa* predominant over the yellow which is vestigial; in pigmentation *C. botrytis* is complementary to the Flava-group, but its spores are longer, on the average, and smooth, though finely and innately striate (Fig. 2). This striation can be seen on the immature spores of *C. formosa* and *C. flava* before they roughen. The sporograph of *C. botrytis* (*B* in Graph 2) seems to be merely the extension of the *formosa*-locus.

C. fragillima and *C. cyanocephala* are tropical species with much darker brown spores which are densely echinulate and relatively wider (Fig. 2). The spore measurements refer to the spore-body without the spines. Their loci are distinctly different from that of *C. formosa*. *C. Invalii* and *C. nigrescens* are two palaearctic species related to *C. fragillima* and their widely separate species-points confirm the *fragillima*-locus. The divergence of the *cyanocephala*-locus is caused by the fact that this species is disporous, and 2-spored basidia always produce slightly wider spores than similar 4-spored basidia; indeed, if

Table 4. *Sporograph data for Clavaria aurea and related species*

Species	Range of spore size ($D \times d$) in μ	Range of D (μ)	Averages of ranges in D			
			D (μ)	d (μ)	E	No. of records
<i>C. aurea</i>	11.0-15.5 \times 4.0-5.5	11.0-11.5	11.35	4.74	2.39	10
		12.0-12.5	12.15	4.72	2.57	10
		13.0-13.5	13.25	4.97	2.67	10
		14.0-14.5	14.15	5.08	2.79	10
		15.0-15.5	15.05	5.14	2.93	10
		—	12.8	5.0	2.56	Auctt.* (29)
<i>C. botrytis</i>	8.0-15.0 \times 3.0-6.0 14.0-20.0 \times 4.5-6.0	14.0-14.5	14.40	4.97	2.90	10
		15.0-15.5	15.15	5.03	3.01	10
		16.0-16.5	16.05	5.27	3.04	10
		17.0-17.5	17.10	4.97	3.44	10
		18.0-20.0	19.00	5.20	3.66	4
		—	14.5	5.0	2.90	Auctt.* (7)
<i>C. flava</i>	11.0-18.0 \times 4.0-6.0 11.0-20.0 \times 4.0-6.5	11.0-11.5	11.17	4.83	2.31	3
		12.0-12.5	12.18	4.94	2.36	19
		13.0-13.5	13.31	5.01	2.60	29
		14.0-14.5	14.16	4.99	2.84	23
		15.0-15.5	15.12	5.32	2.84	25
		16.0-16.5	16.20	5.25	3.09	25
		17.0-17.5	17.21	5.35	3.22	12
		18.0-18.5	18.10	6.10	2.97	5
		19.0-19.5	19.13	5.45	3.51	4
		20.0	20.00	5.63	3.58	4
<i>C. fragillima</i>	10.0-16.0 \times 4.7-7.5	10.0-10.5	10.20	4.97	2.05	10
		11.0-11.5	11.25	5.59	2.01	20
		12.0-12.5	12.10	5.73	2.11	20
		13.0-13.5	13.20	5.75	2.30	20
		14.0-14.5	14.15	6.14	2.30	20
		15.0-15.5	15.20	6.08	2.50	20
<i>C. cyanocephala</i>	11.0-17.5 \times 6.0-10.0	11.0-11.5	11.40	7.32	1.56	20
		12.0-12.5	12.20	7.67	1.59	30
		13.0-13.5	13.33	7.71	1.73	30
		14.0-14.5	14.15	8.02	1.76	30
		15.0-15.5	15.05	8.03	1.88	20
		16.0-17.5	16.40	9.07	1.81	10
		—	7.58	4.10	1.85	Auctt.* (12)
		—	15.5	6.4	2.42	Auctt.* (5)
<i>C. Invalii</i>	6.0-10.5 \times 3.5-5.0	—	—	—	—	—
<i>C. nigrescens</i>	12.5-20.0 \times 5.0-8.0	—	—	—	—	—

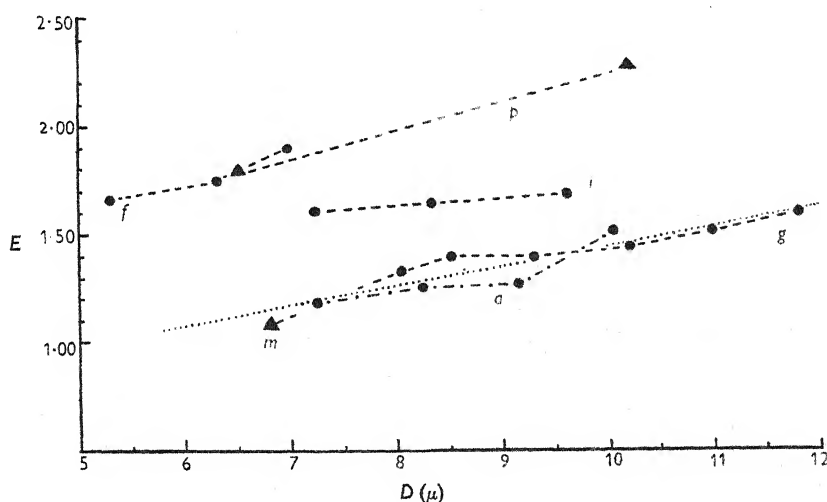
* Averages of the mean values of spore records given by various authors, the number of records in brackets.



Graph 3. Sporograph of *Clavaria aurea* (A, with black circles), *C. flava* (white circles), *C. fragillima* (R), and *C. cyanocephala* (Y), I and N being the species-points for *C. Invalii* and *C. nigrescens*; a, the species-point for *C. aurea*. The broken lines represent the loci.

these spores are transformed to tetraspores, the *cianocephala*-locus appears identical with that of *C. fragillima* (the aberration of the largest spores of *C. cianocephala* is caused by the fact that they are monospores).

Clearly, as more species are studied, a *generic sporograph* must be made to compare the different species-lines. These lines show how spores of the same kind change shape as they grow larger. The generic sporograph will show the different kinds of spores in the genus with their different manners of growth. In the generic sporograph, the species-lines will converge to the base-line (E as unity), when D is $c. 2\mu$; thus it will be necessary to study carefully the species with large spores, where differences are well displayed, or fanned out, before one can hope to assign the species with smaller spores to their appropriate loci in the confusion near the convergence.



Graph 4. Sporograph of *Clavaria acuta* (a), *C. Gibbsiae* (g), *C. Gibbsiae* f. *microspora* (m), *C. incarnata* (i), *C. fumosa* (f) and *C. purpurea* (p) with its 'giant spore', the dotted line being the species-line for *C. acuta* and *C. Gibbsiae*.

Clavaria acuta, *C. Gibbsiae*, *C. incarnata*, *C. fumosa* and *C. purpurea* (Table 5). These species with smooth colourless spores belong to a widely different group of *Clavaria*. Their loci or species-points are shown in Graph 4, which, as a generic sporograph, displays three kinds of spore. *C. acuta* (north temperate) and *C. Gibbsiae* (tropical Asia) are very closely related, with broadly ellipsoid spores suggesting that E may be unity when D is $4-5\mu$. Thus, *C. Gibbsiae* f. *microspora* has subglobose spores $6-7\mu$, and an allied species with globose spores $3-4\mu$ may well exist. *C. fumosa*, in contrast, shows a narrowly ellipsoid spore, and it is remarkable that the spores of the allied *C. purpurea* conform almost exactly with the *fumosa*-locus. The spores of *C. purpurea* are, usually, like those of *C. fumosa*, if a little larger, but it generally produces also in small numbers so-called giant-spores $8-15\mu$ long, which are puzzling and have been regarded as abnormal; the sporograph shows that they are merely larger spores of the same kind as the normal spores but, probably, borne on longer basidia with a greater volume (in fact, on basidia transitional to the cystidia which occur in this species; see later). The *incarnata*-locus represents the ordinary ellipsoid spore of small size. It may intersect the *fumosa*-locus at

Table 5. *Sporograph data for white-spored species of Clavaria and for Typhula phacorrhiza*

Species	Range of spore size ($D \times d$) in μ	Range in D (μ)	Averages of ranges in D			
			D (μ)	d (μ)	E	No. of spores
<i>C. acuta</i>	6.5-10.3 \times 5.0-8.0	7.0-7.5 8.0-8.5 9.0-9.5 10.0-10.3	7.25 8.25 9.15 10.04	6.14 6.55 7.15 6.60	1.18 1.26 1.28 1.52	10 15 10 7
<i>C. Gibbsiae</i>	7.7-12.5 \times 5.5-8.5	8.0-8.3 8.5-8.7 9.0-9.7 10.0-10.5 11.0 11.5-12.5	8.05 8.52 9.30 10.20 11.00 11.80	6.05 6.09 6.64 7.03 7.02 7.28	1.33 1.40 1.40 1.45 1.53 1.62	6 11 14 29 7 5
<i>f. microspora</i>	6.0-7.5 \times 5.5-7.0	—	6.8	6.3	1.08	Mean
<i>C. incarnata</i>	6.5-10.0 \times 3.5-6.5	6.5-7.5 8.0-8.5 9.0-10.0	7.21 8.33 9.61	4.48 5.05 5.65	1.61 1.65 1.70	14 27 13
<i>C. fumosa</i>	5.0-7.0 \times 3.0-4.0	5.0-5.5 6.0-6.5 6.7-7.0	5.30 6.30 6.97	3.19 3.60 3.67	1.66 1.75 1.90	20 20 10
<i>C. purpurea</i> , 'giant spores'	5.0-7.5 \times 3.0-4.2 8.0-13.0 \times 3.5-5.0	— —	6.5 10.20	3.6 4.43	1.8 2.30	Av. Av.
<i>C. fusiformis</i>	6.5-9.0 \times 6.0-8.5	6.5-7.5 8.0-8.7 9.0	7.18 8.23 9.0	6.24 7.35 8.0	1.15 1.12 1.12	21 25 4
<i>C. rugosa</i>	9.0-13.0 \times 7.0-10.0	9.0-10.0 10.5 11.0 11.5 12.0 12.5-13.0	10.0 10.5 11.0 11.5 12.0 12.7	8.57 8.7 9.0 9.2 9.2 9.3	1.18 1.21 1.23 1.25 1.30 1.37	15 7 9 13 19 3
<i>C. pistillaris</i>	11.0-14.5 \times 6.7-9.5	11.0-11.5 12.0-12.5 13.0-13.5 14.0-14.5	11.35 12.20 13.30 14.18	7.27 7.53 7.78 7.97	1.56 1.62 1.71 1.78	20 20 20 20
Europe	9.0-16.0 \times 5.0-10.0	—	13.0	7.3	1.78	Auctt.
America	7.2-12.5 \times 3.7-7.0	—	9.8	5.5	1.78	Auctt.
<i>C. juncea</i>	6.0-12.0 \times 3.0-5.0	—	9.1	4.4	2.07	Auctt.
	10-12 \times 5	—	11.0	5.0	2.20	Karsten
	10-12 \times 4.5	—	11.0	4.5	2.44	Corner
	9-12 \times 4.5	—	10.5	4.5	2.33	Harper
	9-10 \times 3.8-4.5	—	9.5	4.2	2.29	Doty
	8-11 \times 4.5	—	9.5	4.5	2.11	Cotton
	8-12 \times 4.5	—	9.0	4.5	2.20	Burt
	7-10 \times 3.5	—	8.5	4.0	2.13	Bourdot
	8-9 \times 4.5	—	8.5	4.5	1.89	Rea
	6.5-10 \times 4.5	—	8.3	4.5	1.83	Donk
	6-10 \times 3.2-4.5	—	8.0	4.0	2.00	Lundell
	7-9 \times 3.5-5	—	8.0	4.25	1.88	Bresad.
	6-9.3 \times 3.8-4.8	—	7.7	4.3	1.78	Coker
	5.5-7.0 \times 3.7-4	—	6.3	3.85	1.62	Cleland
<i>Typhula phacorrhiza</i>	11.0-20.0 \times 4.7-7.5	11.0-11.5 12.0-12.5 13.0-13.5 14.0-14.5 15.0-15.5 16.0-16.5 17.0-18.0 20.0	11.17 12.03 13.26 14.25 15.20 16.10 17.20 20.0	5.40 5.95 6.18 6.19 6.21 6.74 7.15 7.0	2.07 2.02 2.14 2.30 2.45 2.39 2.41 2.9	3 10 10 10 10 10 10 1
	9-10 \times 4.5	—	9.5	4.5	2.1	Bourdot
	10-12 \times 4.6	—	11.0	5.0	2.2	Buller
	9-14 \times 4.6	—	11.5	5.0	2.3	Coker
	9.7-13.5 \times 4.8	—	11.6	6.0	1.9	Remsburg
	9.5-14 \times 5.5	—	11.8	5.5	2.1	Donk
	12-14 \times 5.6	—	13.0	5.5	2.4	Lundell

Locus for *C. acuta*-*C. Gibbsiae*: 5.8:1.05-12.0:1.65

Locus for *C. incarnata*: 7.1:1.6-9.6:1.7

Locus for *C. fumosa*: 5.3:1.65-7.0:1.85

Locus for *C. fusiformis*: 6.0:1.12-9.0:1.12

Locus for *C. rugosa*: 9.5:1.15-13.0:1.35

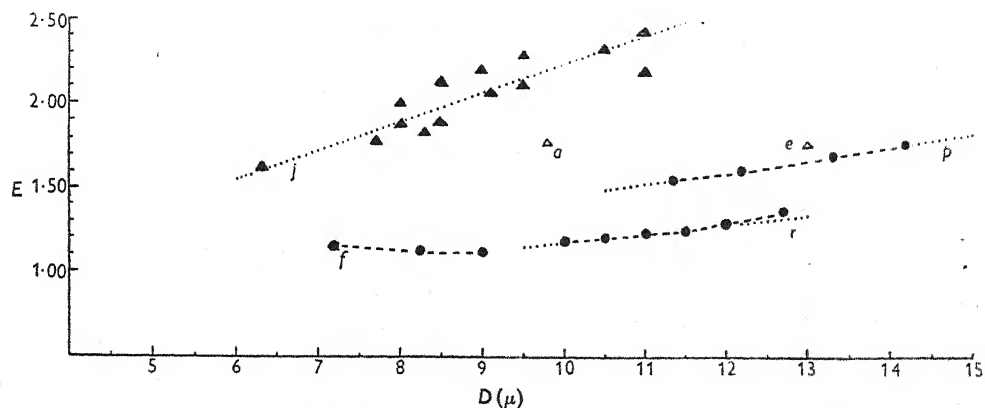
Locus for *C. pistillaris*: 10.5:1.50-15.0:1.85

Locus for *C. juncea*: 6.0:1.55-11.5:2.50

Locus for *Typhula phacorrhiza*: 9.5:1.95-20.0:2.70

$D=4$ or 5, and it thus shows that one may expect species with spores of the same average size and shape but belonging to different kinds, or loci, as a spurious resemblance which only the extended analysis of the sporograph can resolve; in other words, developmental analysis is needed to understand adult structure in organisms.

Clavaria rugosa and *C. fusiformis* (Table 5). These species are not closely related but both have subglobose spores. Sporographic analysis (Graph 5) shows that the spores of *C. rugosa* slowly become ellipsoid as they grow, whereas those of *C. fusiformis* are constantly subglobose. Probably few species have truly globose spores.



Graph 5. Sporograph of *Clavaria fusiformis* (f), *C. rugosa* (r), *C. juncea* (j) and *C. pistillaris* (p); a, species-point for American specimens of *C. pistillaris*; e, species-point for European specimens of *C. pistillaris*; the dotted lines being the species-lines.

Clavaria pistillaris and *C. juncea* (Table 5). The colourless spores of both these species are so much alike in shape and contents that one might consider those of *C. juncea* to differ from those of *C. pistillaris* merely in being about two-thirds as large. The sporograph (Graph 5) shows, however, that there is no such relation between them, for it would imply a horizontal line with constant value for E ; instead, their spores conform to separate, and not even parallel, loci. That for *C. juncea* is derived entirely from species-points which, nevertheless, indicate a band for which the dotted line in Graph 5 may be taken provisionally as the mid-line. As with *C. conjunctipes* var. *odora* and *C. formosa*, so in this case the sporograph links the very short spores given by Cleland for *C. juncea* in Australia with those typical of north temperate countries. In contrast, the point for the North American collections of *C. pistillaris* differs widely from that for the European; it suggests an intermediate locus between *C. juncea* and *C. pistillaris* which is probably the locus for *C. ligula* and *C. fistulosa*.

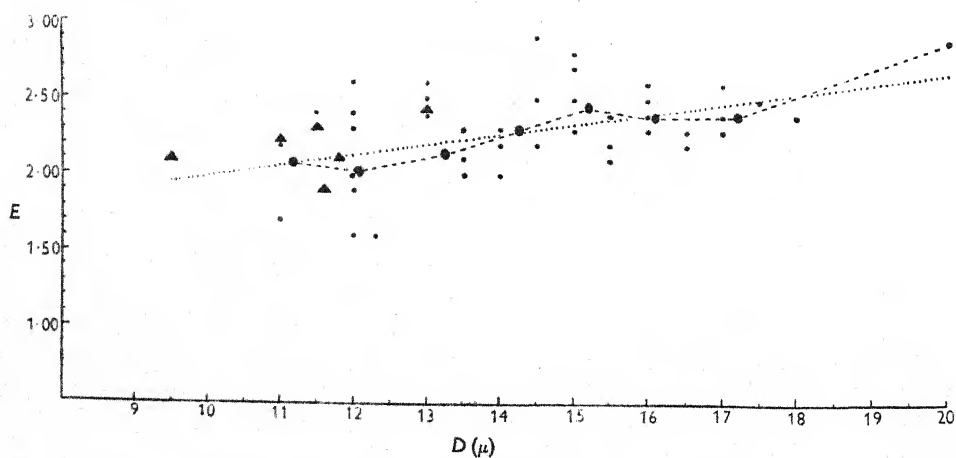
Typhula phacorrhiza. Descriptions of species of *Typhula* imply that spore-size is specific. The sporograph of *T. phacorrhiza* (Graph 6, Tables 5 and 6) shows such range and latitude that one cannot accept any specificity for the large spores of such as *T. intermedia*, *T. variabilis*, *T. incarnata*, and so on, until they have been analysed in detail. Similarly, the small-spored species ($D=5-10\mu$) appear to fit the same locus without specific distinction.

Boletus. The smooth, coloured, elongate spores of *Boletus* are suitable for precise measurement. I have tested the species-locus in some twenty Malayan species, the

results for nine of which are summarized in Tables 7 and 8 and in Graphs 7 and 8. (I have been unable to get specific names for most of these as yet, and so I have used my manuscript symbols for reference.) I have already commented on the regular variation of the

Table 6. *Spore size in a fruit-body of Typhula phacorrhiza*

$D \times d (\mu)$	E	No. of spores	$D \times d (\mu)$	E	No. of spores
11.0 × 5.0	2.2	1	14.5 × 6.5	2.2	2
11.0 × 6.5	1.7	1	14.5 × 6.7	2.2	1
11.5 × 4.7	2.4	1	15.0 × 5.3	2.8	2
12.0 × 4.7	2.6	1	15.0 × 5.5	2.7	1
12.0 × 5.0	2.4	2	15.0 × 6.0	2.5	2
12.0 × 5.3	2.3	1	15.0 × 6.5	2.3	1
12.0 × 6.0	2.0	3	15.5 × 6.5	2.4	2
12.0 × 6.5	1.8	1	15.5 × 7.0	2.2	1
12.0 × 7.5	1.6	1	15.5 × 7.5	2.1	1
12.3 × 7.5	1.6	1	16.0 × 6.0	2.6	2
13.0 × 5.0	2.6	2	16.0 × 6.5	2.5	1
13.0 × 5.3	2.5	1	16.0 × 6.7	2.4	3
13.0 × 7.0	1.9	1	16.0 × 7.0	2.3	2
13.5 × 6.0	2.3	1	16.5 × 7.3	2.3	1
13.5 × 6.5	2.1	3	16.5 × 7.5	2.2	1
13.5 × 7.0	2.0	2	17.0 × 6.5	2.6	1
14.0 × 6.0	2.3	3	17.0 × 7.0	2.4	4
14.0 × 6.5	2.2	1	17.0 × 7.5	2.3	2
14.0 × 7.0	2.0	1	17.5 × 7.0	2.5	2
14.5 × 5.0	2.9	1	18.0 × 7.5	2.4	1
14.5 × 5.7	2.5	1	20.0 × 7.0	2.9	1



Graph 6. Sporograph of *Typhula phacorrhiza* showing the individual points of Table 6, the average points of Table 5, and the species-points (triangles) of Table 5, the dotted line being the species-line.

spores of *B. funerarius*. It is worth noting, also, that when measuring its spores at random, I found that the column for spores 12.0–12.8 μ long filled up most quickly, and that by the time there were twenty in it, out of a total of thirty-three measured spores, these twenty gave the average figures 12.5 × 5.82 μ ($E = 2.16$), which agree closely with the final results.

Table 7. *Sporograph data for Boletus (spore size in μ)*

Species	Total range of spore size, $D \times d$	Range in D	Averages of ranges in D			
			D	d	E	No. of spores
<i>Boletus</i> '64'	4.3- 7.0 \times 2.5-3.4	4.3-4.8 5.0- 5.3	4.60 5.14	2.77 3.03	1.66 1.70	20 20
<i>Boletus</i> '8'	5.0- 6.7 \times 3.5-4.3	5.5- 7.0 5.5-5.7 6.0- 6.7	5.93 5.49 6.20	3.11 3.72 4.05	1.91 1.48 1.53	21 20 20
<i>Boletus</i> '3c'	7.0- 9.0 \times 4.3-5.2	(5.0- 6.7 7.0- 7.7 8.0- 8.7 9.0	5.85 7.41 8.23 9.00	3.89 4.75 5.02 5.10	1.50 1.56 1.64 1.76	40 20 20 6
<i>B. funerarius</i>	10.0-14.7 \times 5.0-6.5	10.0-10.7 11.0-11.7 12.0-12.7 13.0-13.7 14.0-14.7	10.44 11.54 12.42 13.21 14.20	5.17 5.44 5.72 6.00 6.35	2.02 2.12 2.17 2.20 2.24	11 50 101 50 6
<i>Boletus</i> '19b'	13.5-15.0 \times 6.0-7.0	13.5-13.7 14.0-14.7 15.0	13.57 14.06 15.0	6.25 6.39 6.58	2.17 2.20 2.28	6 10 4
<i>Boletus</i> '4'	12.0-18.3 \times 4.0-5.2	12.0-12.7 13-13.7 14.0-14.7 15.0-15.7 16.0-16.7 17.0 18.3	12.30 13.38 14.50 15.22 16.20 17.0 18.3	4.68 4.55 4.65 4.79 4.90 5.0 5.0	2.63 2.94 3.12 3.18 3.31 3.40 3.7	4 20 20 20 20 6 1
<i>Boletus</i> '42f'	10.0-21.0 \times 4.3-6.7	10.0-10.5 11.0-11.7 12.0-12.7 13.0-13.7 14.0-14.7 15.0-15.7 16.0-16.7 17.0-17.7 18.0-18.7 19.0-19.3 20.0 21.0	10.25 11.43 12.38 13.30 14.33 15.11 16.46 17.22 18.10 19.10 20.0 21.0	4.50 4.50 4.68 4.81 5.00 5.10 5.16 5.17 5.29 5.73 5.37 5.5	2.28 2.54 2.65 2.77 2.87 2.96 3.19 3.33 3.42 3.33 3.72 3.82	2 7 13 20 20 20 20 20 20 3 3 1
<i>Boletus</i> '62'	15.0-21.5 \times 5.5-7.7	15.0-15.7 16.0-16.7 17.0-17.7 18.0-18.7 19.0-19.7 20.0-20.7 21.0-21.5	15.33 16.37 17.26 18.27 19.32 20.12 21.17	5.89 6.13 6.42 6.59 6.85 7.10 7.17	2.60 2.67 2.69 2.77 2.82 2.83 2.95	14 20 20 20 20 20 3
<i>Boletus</i> '50a'	16.0-20.0 \times 7.7-9.0	16.0-16.7 17.0-17.7 18.0-18.7 19.0 20.0	16.35 17.29 18.06 19.00 20.00	7.94 8.19 8.36 8.71 8.70	2.06 2.11 2.16 2.18 2.30	6 10 10 2 2

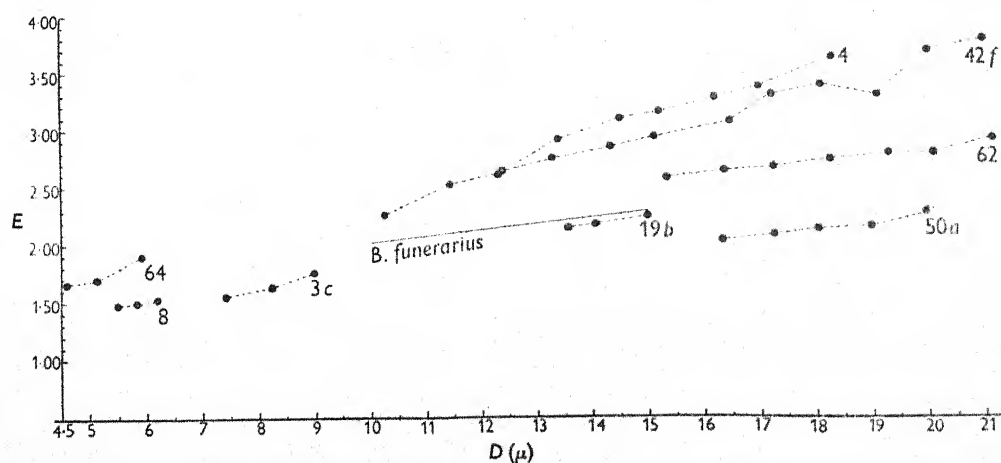
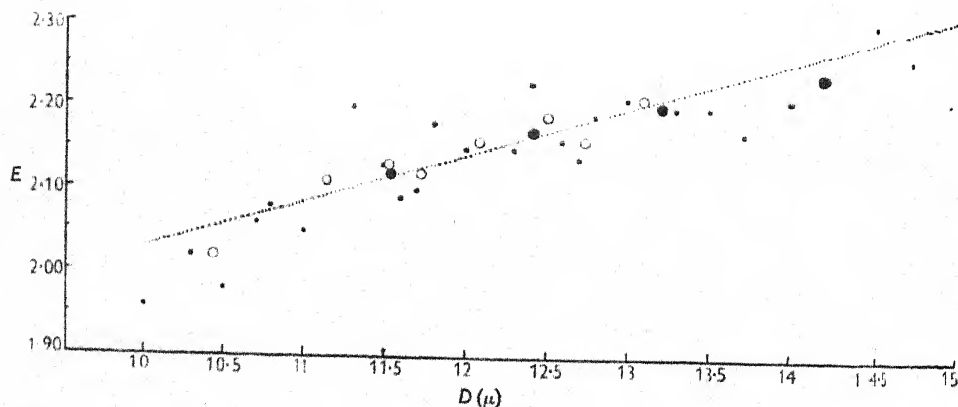
Graph 7. Sporograph of nine species of *Boletus*, as in Table 7, *B. funerarius* shown as a species-line derived from Graph 8.

Table 8. *Sporograph data for Boletus funerarius*

Spore range (μ)	No. of spores	Average size (μ)	Average E
10 × 5.5.2	2	10.0 × 5.1	1.96
10.3 × 5.5.3	3	10.3 × 5.1	2.02
10.5 × 5.3	2	10.5 × 5.3	1.98
10.7 × 5.5.3	3	10.7 × 5.2	2.06
10.8 × 5.2	1	10.8 × 5.2	2.08
11.0 × 5.5.7	5	11.0 × 5.4	2.05
11.3 × 5.5.2	4	11.3 × 5.2	2.20
11.5 × 5.5.7	17	11.5 × 5.4	2.13
11.6 × 5.5.5.6	2	11.6 × 5.6	2.09
11.7 × 5.2.6.0	18	11.7 × 5.6	2.10
11.8 × 5.3.5.5	4	11.8 × 5.4	2.18
12.0 × 5.3.6.2	28	12.0 × 5.6	2.15
12.3 × 5.3.6.3	18	12.3 × 5.7	2.15
12.4 × 5.4.5.7	2	12.4 × 5.6	2.23
12.5 × 5.4.6.3	22	12.5 × 5.7	2.19
12.6 × 5.7.6.0	3	12.6 × 5.8	2.16
12.7 × 5.7.6.2	17	12.7 × 5.9	2.14
12.8 × 5.3.6.3	11	12.8 × 5.8	2.19
13.0 × 5.6.6.3	25	13.0 × 5.9	2.21
13.2 × 6.0	2	13.2 × 6.0	2.20
13.3 × 5.7.6.5	10	13.3 × 6.1	2.20
13.5 × 5.7.6.5	9	13.5 × 6.1	2.20
13.7 × 6.2.6.5	4	13.7 × 6.3	2.17
14.0 × 6.2.6.5	4	14 × 6.3	2.21
14.5 × 6.3	1	14.5 × 6.3	2.30
14.7 × 6.5	1	14.7 × 6.5	2.26
10-10.8 × 5.5.3	11	10.44 × 5.17	2.02
11-11.3 × 5.5.7	9	11.13 × 5.27	2.11
11.5-11.7 × 5.5.7	19	11.52 × 5.41	2.13
11.7-11.8 × 5.2.6.0	22	11.72 × 5.54	2.12
12-12.3 × 5.3.6.3	46	12.18 × 5.65	2.16
12.4-12.6 × 5.4.6.3	27	12.50 × 5.70	2.19
12.7-12.8 × 5.3.6.3	28	12.74 × 5.89	2.16
13-13.3 × 5.6.6.5	37	13.09 × 5.93	2.21

(The remainder as above)

Locus: 0: 1.48-15.0: 2.31.

Graph 8. Sporograph of *Boletus funerarius*, from the data in Table 8, showing the effect of progressive averaging, the dotted line being the inferred species-line.

DEVELOPING SPORES

The sporograph of *Boletus* shows that the species-locus for mature spores is a straight line. Continuation of this line to the axis of the graph would appear to represent the growth of the spore on the sterigma. The level with *E* as unity may be the base-line in most cases, but there are certainly spores which at their very beginning are wider than long. At this stage it is difficult to know how to measure them (Figs. 1*d*, 3*h*) and they must be studied from the superposition of camera lucida drawings of their actual growth. I have been able

Table 9. *Mature and developing spores of Typhula hyalina*

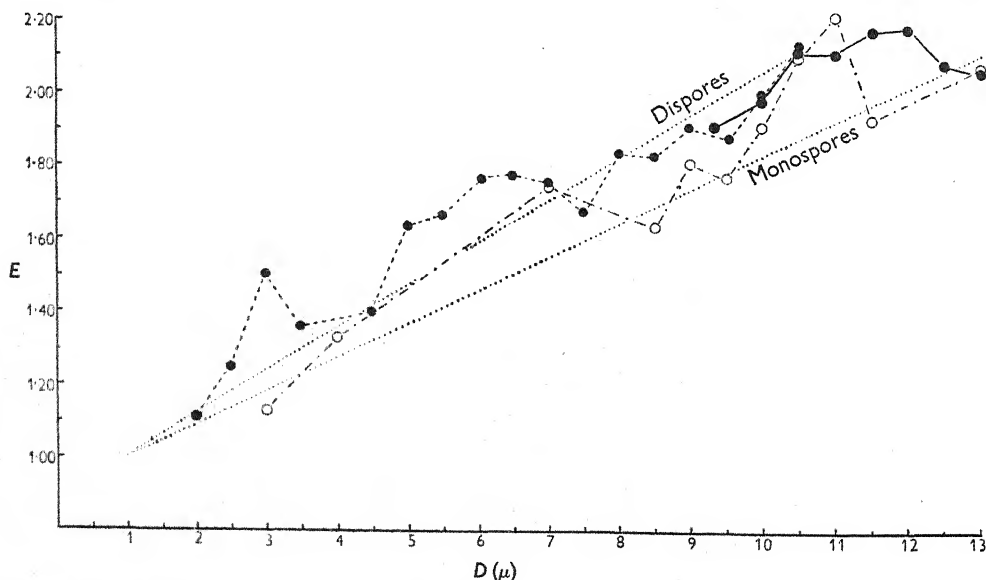
Spore range in μ	Range of <i>D</i> (μ)	Averages for ranges in <i>D</i>		
		<i>D</i>	<i>E</i>	No. of spores
Mature spores: 9.0-13.0 \times 4.5-7.0	9.0-9.5	9.33	1.90	3
	10.0	10.0	1.97	10
	10.5	10.5	2.10	4
	11.0	11.0	2.10	5
	11.5	11.5	2.16	5
	12.0	12.0	2.17	9
	12.5	12.5	2.07	3
	13.0	13.0	2.05	2
Dispores: 9.0-10.5 \times 4.0-5.7	2.0	2.0	1.11	4
	2.5	2.5	1.25	4
	3.0	3.0	1.50	4
	3.5	3.5	1.36	6
	4.5	4.5	1.40	4
	5.0	5.0	1.63	6
	5.5	5.5	1.66	6
	6.0-6.3	6.06	1.76	10
	6.5	6.5	1.77	8
	7.0	7.0	1.75	4
	7.5	7.5	1.67	6
	8.0-8.3	8.01	1.83	18
	8.5	8.5	1.82	16
	9.0	9.0	1.90	18
	9.5-9.7	9.54	1.87	10
	10.0	10.0	1.99	14
	10.5	10.5	2.12	16
Monospores: 11.0-13.0 \times 5.0-7.0	3.0	3.0	1.13	2
	4.0	4.0	1.33	1
	7.0	7.0	1.75	2
	8.5	8.5	1.63	1
	9.0	9.0	1.80	2
	9.5	9.5	1.76	3
	10.0	10.0	1.90	1
	10.5	10.5	2.10	1
	11.0	11.0	2.20	2
	11.5	11.5	1.92	2
	13.0	13.0	2.06	2

Locus for dispores: 1.0 : 1.00-10.5 : 2.10.

Locus for monospores: 1.0 : 1.00-13.0 : 2.10.

to study developing spores only in one Clavarioid fungus because I have had no recent opportunity to study living material of those for which I have analysed the mature spores; it is, also, a tedious and much more difficult work. The use of species-points, however, enabled me to examine the tropical agaric *Hygrophorus firmus* in this respect. The sporographs of these two fungi indicate that the locus of the mature spores is merely the continuation of that of the developing spores.

Typhula hyalina.* This species has mostly 2-spored basidia, but roughly 5% of the basidia are monosporous; more than two sterigmata are never formed. In Table 9 I give the measurements of some forty mature spores in a spore-print, and those for developing dispores and monospores. The mature spores will have been mostly dispores, but *c.* 2% will have been monospores. The distinction, however, is not sharp because some basidia have two unequally developed spores, one of which becomes a 'partial monospore' in that it develops to maturity while the other aborts at some early stage of growth ($1.5\text{--}5\text{ }\mu$ long). The longest dispores which I found attached to sterigmata were $10.5\text{ }\mu$ long, but monospores reach $13\text{ }\mu$ long; partial monospores have intermediate length. The monospores are, also, slightly broader than the dispores. Hence the species-locus represents



Graph 9. Sporograph of *Typhula hyalina*. The continuous line represents mature spores from a spore-print. The dashed line represents developing dispores. The dot-dashed line represents developing monospores. The dotted lines represent the inferred loci for dispores and monospores. (Note that the scale of *E* is double that in the preceding graphs.)

dispores from $D = 9.0$ to $D = 10.5$; then, as a mixture of partial and complete monospores, it falls away to $D = 13.0$. At maturity the spore-wall thickens slightly and, by this means, it was possible to decide that mature monospores were $11.0\text{--}13.0\text{ }\mu$ long. The data for developing spores suggest that in both cases the spores lengthen more rapidly from $D = 4.5$ to $D = 7.0$, so that the locus for the developing spores may be a curve rather than a straight line. The explanation of this anomaly is to be sought in the vacuolar pressure of the basidium which discharges the protoplasm into the spores and which reaches a maximum about this period of their growth, when the tangential expansion of the spore-wall is declining. The anomaly will be more pronounced in monospores than in dispores and, perhaps, non-existent in tetraspores which offer four outlets for the basidial pressure. Such problems must be deferred until the study of the basidium unit, but it is opportune to point out that the simplicity of the straight line for the locus on the sporograph, if only

* This species of Malaya and Java is allied with the European *Pistillaria setipes* but has several oddities, as thick-walled cystidia, for which I propose to make it the type of a new genus.

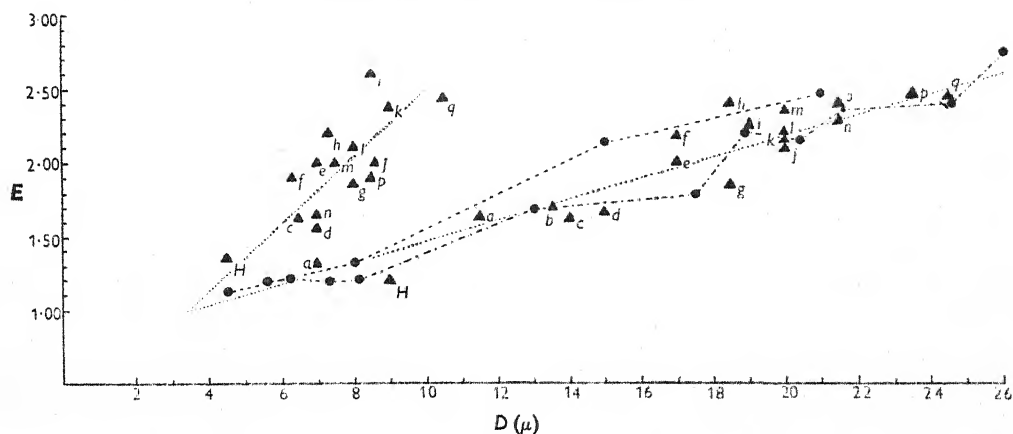
as a means of analysis, discovers such details which might easily be overlooked. Certainly, the developing spores do not enlarge uniformly in length and width, in which case *E* would be constant, but show longitudinal growth increasing over tangential, just as the mature spores indicate in their variation in size.

Table 10. *Sporograph data (species-points) for Hygrophorus firmus and H. hypohaemactus*

	Graph ref.	Macrospores		Microspores	
		<i>D</i>	<i>E</i>	<i>D</i>	<i>E</i>
<i>H. hypohaemactus</i>	<i>H</i>	9.0	1.20	4.5	1.36
<i>H. firmus</i>					
var. (unnamed)	<i>a</i>	11.5	1.64	7.0	1.32
var. <i>puniceoides</i>	<i>b</i>	13.5	1.70	—	—
Typical	<i>c</i>	14.0	1.65	6.5	1.63
var. (unnamed)	<i>d</i>	15.0	1.67	7.0	1.56
var. (unnamed)	<i>e</i>	17.0	2.00	7.0	2.00
var. (unnamed)	<i>f</i>	17.0	2.18	6.3	1.90
var. (unnamed)	<i>g</i>	18.5	1.85	8.0	1.86
var. <i>sericeus</i>	<i>h</i>	18.5	2.40	7.3	2.20
var. (unnamed)	<i>i</i>	19.0	2.24	8.5	2.60
var. (unnamed)	<i>j</i>	20.0	2.10	8.6	2.00
var. <i>gracillimus</i>	<i>k</i>	20.0	2.16	9.0	2.37
var. (unnamed)	<i>l</i>	20.0	2.20	8.0	2.10
var. (unnamed)	<i>m</i>	20.0	2.35	7.5	2.00
var. <i>flavus</i>	<i>n</i>	21.5	2.29	7.0	1.65
var. <i>stratiotes</i>	<i>o</i>	21.5	2.40	—	—
var. (unnamed)	<i>p</i>	23.5	2.47	8.5	1.90
var. <i>longipes</i>	<i>q</i>	24.5	2.45	10.5	2.44

Locus for macrospores: 3.4: 1.00-26.0: 2.60.

Locus for microspores: 3.4: 1.00-10.0: 2.50.



Graph 10. Sporograph of *Hygrophorus firmus* and *H. hypohaemactus*. The dotted lines show the inferred loci for micro- and macrospores. The dashed line represents the developing macrospores of *H. firmus* var. *stratiotes*; the dot-dashed line represents the developing macrospores of *H. firmus* var. *flavus*. *H* refers to *H. hypohaemactus*. For other lettering, see Table 10.

Hygrophorus firmus and *H. hypohaemactus* (Corner, 1936). These agarics have dimorphous basidiospores. The large spores, or macrospores, are two to four times as long and wide as the small spores, or microspores, and have roughly ten times the volume (Fig. 1c); the macrospores are produced from much larger basidia than the microspores and intermediates are few. *H. firmus* is extremely variable microscopically, as well as

macroscopically, so that its varieties provide some twenty species-points both for macrospores and microspores, and these can be used in the absence of detailed measurements to examine the relation between the two kinds of spore. I have also a small number of measurements of developing macrospores, as given in Table 11. Graph 10 shows, at once, that the microspores are not juvenile macrospores but spores of another kind, having a widely different locus which would quickly lead to a cylindric fusiform spore (as in species of *Marasmius*). The different sizes of the macrospores in the varieties of *H. firmus* conform with the locus indicated by the developing macrospores, showing that they represent the same kind of spore with variations in extent of development. Doubtless this is the state also with the microspores, but the lengths of the microspores seem not always to correspond with those of the macrospores; thus, the data in Table 10 are arranged for increasing length of the macrospores and lettered accordingly for reference;

Table 11. *Sporograph data for developing macrospores of Hygrophorus firmus*

	Graph ref.	D	E	No. of spores
var. <i>flavus</i>	n	5.6	1.20	2
		6.2	1.22	3
		7.3	1.20	3
		8.1	1.21	3
		13.0	1.69	2
		17.5	1.79	2
		18.9	2.21	8
		20.4	2.15	9
		21.6	2.36	7
		24.6	2.40	3
		26.0	2.74	1*
var. <i>stratiotes</i>	o	4.5	1.13	12
		8.0	1.33	12
		15.0	2.14	12
		21.0	2.47	12

* The largest macrospore.

the microspores do not fall exactly in the same sequence. The two widely separate points (H) for *H. hypohaemactus*, which is a very distinct species, prove the inference from the species-points of *H. firmus* and suggest that its spores represent the most juvenescent of the series. On the other hand, there may be more than one locus for the macrospores of *H. firmus*, corresponding with the subspecific groups *Ovalisporae* and *Macrospora*e mentioned in my paper. Indeed, the sporograph suggests a generic sporograph and I am still undecided whether the two species represent two sections of a new subgenus of *Hygrophorus* and whether some, at least, of the varieties of *H. firmus* should not be treated as species. Clearly, however, for the present purpose, both species have two kinds of spore, unlike *Clavaria purpurea*, which has two sizes of the same kind of spore, and unlike *Typhula hyalina*, which has only one kind of spore modified by the number per basidium.

SIZE, SHAPE AND KIND IN SPORES

It is obviously impossible to speak precisely of the size, shape and kind of basidiospores without reference to the sporograph. The shape of the ellipsoid spore depends on its length, and the globose spore is merely a special case. I suggest, therefore, the following meanings until new words may be found useful.

Spores of the same kind are spores conforming to the same locus on the sporograph, as well as agreeing in other generic features. They need not have the same shape or size. Thus, the spores of *Clavaria formosa* may be $7 \times 3.5 \mu$ to $17 \times 7 \mu$, broadly or narrowly ellipsoid, and still be of the same kind. Other genera may have similar spores and they can be said to belong to the same category, though generically different. Spores of different kinds conform to distinguishable loci, as in *Hygrophorus firmus* and the European and American fungi referred to *Clavaria pistillaris*.

Spores of the same size have the same dimensions but are not necessarily of the same kind.

Spores of the same shape have the same value of *E* but may differ in size and kind. Globose spores, with horizontal locus, are the only spores of the same shape and kind.

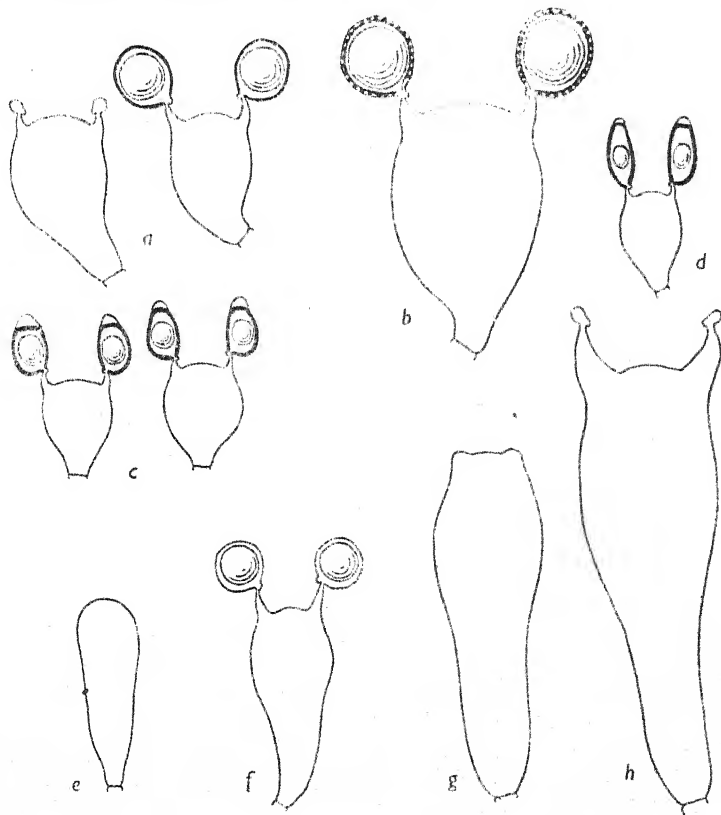


Fig. 3. Basidia mentioned in the text. a, *Amauroderma rugosum*; b, *A. Ramosii*; c, *Ganoderma rivulosum*; d, *Ganoderma* 'A'; e, a young basidium of *Oudemansiella Canarii*; f, *Oudemansiella* sp. 'c'; g, *O. radicata*; h, *O. Canarii* (with spore-rudiments); $\times 800$.

BASIDIA

Having found this graphic manner of relating length and width in the basidiospore, I thought it should be applied to the basidium; for large spores are borne on large basidia and small spores on small basidia. It is, however, difficult to measure accurately the basidia. They do not develop freely and they do not have a common starting-point for reference, though their immature tips may form a fairly level surface. Many basidia

become deformed, with elliptic or irregular cross-section, through mutual compression in the hymenium, and their widths are to be found most accurately by measuring the diameter of the optical outline of the basidium as seen in end-view (from the apex); thus, compressed basidia can be avoided, but lengths cannot be measured. For this purpose, sections of the hymenium must be examined, and it will be seen that the basidia arise at different levels in the subhymenium and reach a common form of maximum width when their apices reach the hymenial level; thus, length is not initially a primary function of shape. Further, these stalks of the basidia, especially among Clavarioid fungi, are hypha-like and frequently curved round the stalks of others or round the subhymenial hyphae, so that accurate measurements of length can rarely be made. Accordingly, I have relied on the principle of the species-point as the fundamental datum, in the absence of any other means of obtaining average values. In the case of one agaric, *Oudemansiella Canarii*,* and a polypore, *Ganoderma rivulosum*, I have been able to obtain average data which compare favourably with their species-points.

Clavaria sensu lato. The basidia of *C. acuta*, *C. vermicularis*, *C. fusiformis*, *C. corniculata*, *C. cristata*, *C. formosa*, *C. stricta*, and their immediate allies are typically elongate and narrowly clavate with hypha-like stalks. Most published measurements are too short, evidently because of the difficulty in seeing the base of the basidium, or they are too long because the thickened hymenium has been measured instead of the individual basidia. I have, therefore, relied mainly on my own records and give in Table 12 the summary of

Table 12. Average data for the length (*l*) and width (*w*) of the basidia of Clavarioid fungi (= *Clavaria sensu lato*)

Range in <i>l</i> (μ)	Averages for ranges in <i>l</i>		
	<i>l</i> \times <i>w</i> (μ)	<i>l</i> / <i>w</i>	No. of species
60-80	65.53 \times 8.32	7.88	19
50-59	51.92 \times 7.86	6.61	20
40-49	43.50 \times 7.22	6.03	21
30-39	34.21 \times 6.32	5.41	22
20-29	24.58 \times 5.51	4.46	22
10-19	14.85 \times 4.07	3.65	4

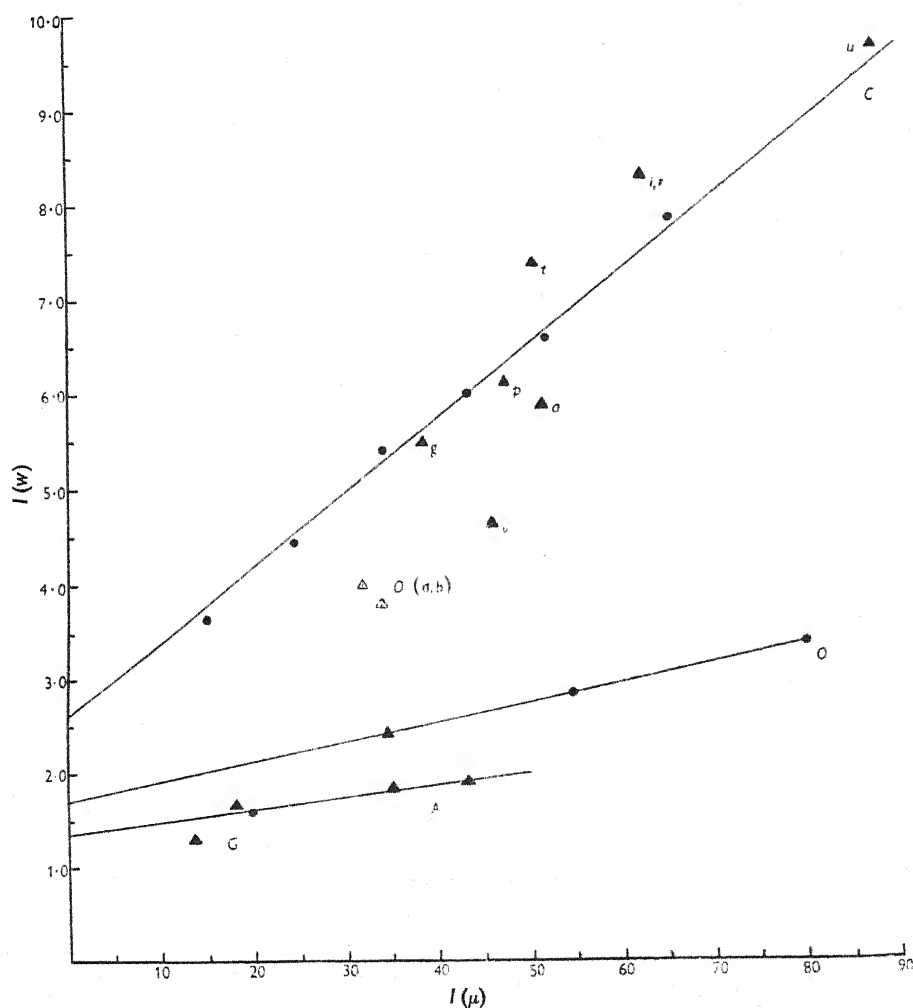
the more accurate data for 108 species of this general alliance. I grouped the mean values of length and width of the basidium for each species according to ranges in length and averaged the values; it is unnecessary to give the many details here because they will be published with the general monograph on these fungi. For convenience, I call the length of the basidium *l* and the width *w*.†

These average or working data, when plotted as a *basidiograph* in the same way as a sporograph, conform to a straight line as a common locus for this kind of basidium (Graph 11). I have since obtained accurate limits for the living basidia of some European species which I had not studied, as always necessary in measuring basidia, from living

* This is the species about which I wrote under its synonym *Collybia apalosarca* (1934); for a full synonymy, see Singer (1945). The species is closely related with *Oudemansiella radicata* (= *Collybia radicata*) and *Oudemansiella mucida* (= *Armillaria mucida*).

† The same symbols cannot be used for the basidium as for the spores because further analysis, into which I cannot go here, shows that *d* is related with *w* and that *D* is related with the volume of the basidium and thus with *l* and *w*.

material; I have indicated these new data separately on the basidiograph. They agree so well as to be proof of the generalized form of the locus, but the new point for *C. Invalii* (*v*) is aberrant. There is no doubt that the line should be expanded into a band, or detailed as several narrowly diverging lines, when there is more accurate information about groups of



Graph 11. Basidiograph of *Clavaria* (C), *Oudemansiella* (O), and *Amauroderma-Ganoderma* (A, G), from Tables 12 and 13. Species-points: a, *Clavaria acuta*; g, *C. gracilis*; i, *C. incarnata*; p, *C. pulchra*; r, *C. argillacea*; t, *C. luteo-alba*; u, *C. umbrinella*; v, *C. Invalii*; O (a, b), *Oudemansiella* spp. a and b.

closely allied species, just as with the sporograph loci. However, the locus serves to compare the narrowly clavate, elongate *Clavaria*-basidium, so hypha-like when young, with the broad basidia of *Oudemansiella* and *Amauroderma*, and to emphasize its peculiarities as a particular kind of basidium.

Oudemansiella. The data for five Malayan species are given in Table 13, and their analysis in Graph 11. The three points joined by the straight line O are those of

O. Canarii, *O. radicata* (Malayan specimens) and the 'species c'.* The two species 'a' and 'b', with short basidia, seem aberrant and conform with the *Clavaria*-locus.

Table 13. *Basidiograph data for the length (l) and width (w) of the basidium in Oudemansiella, Amauroderma and Ganoderma*

Species	Range of basidium $l \times w (\mu)$	Average or mean		No. of basidia
		$l \times w (\mu)$	l/w	
<i>O. Canarii</i>	62.0-98.5 \times 20.3-27.5	80.0 \times 23.5	3.40	20
<i>O. radicata</i>	49.0-60.5 \times 18.2-20.0	54.5 \times 19.1	2.86	15
<i>Oudem. sp. c</i>	30.0-39.0 \times 12.5-16.0	34.5 \times 14.3	2.41	Mean
<i>Oudem. sp. b</i>	—	34.0 \times 8.8	3.86	Mean
<i>Oudem. sp. a</i>	—	32.0 \times 8.0	4.00	Mean
<i>A. Ramosii</i>	35.0-51.0 \times 18.0-27.0	43.0 \times 22.5	1.91	Mean
<i>A. rugosum</i>	24.0-46.0 \times 15.0-23.0	35.0 \times 19.0	1.84	Mean
<i>G. rivulosum</i>	17.0-24.0 \times 10.5-15.0	20.5 \times 12.75	1.61	Mean
<i>G. rivulosum</i>	17.0-24.0 \times 10.5-15.0	19.74 \times 12.50	1.58	55
<i>Ganod. sp. A</i>	16.0-20.0 \times 10.0-11.5	18.0 \times 10.75	1.67	Mean
<i>G. applanatum</i> *	12-15 \times 9-12	13.5 \times 10.5	1.29	Mean

* From Bourdot & Galzin (*Hym. Fr.* 1928).

Amauroderma, *Ganoderma*. The two common Malayan species of *Amauroderma* (Polyporaceae) have the most widely clavate basidia that I have seen. Having found but two species with sufficiently different sizes of basidia, a separate locus for them on the basidiograph would seem barely justifiable (Graph 11), and there appear to be no published data. It occurred to me to test this minimum locus rigorously with data from *Ganoderma*, which is certainly close to *Amauroderma* in general characters but has much smaller spores. *Ganoderma*, therefore, should supply the data for the short basidia which will extend the *Amauroderma*-locus to the origin. Unfortunately, like most mycologists, I had never looked at the basidia of these singularly ugly fungi, so hard and unamenable to the razor, and the only accurate measurements that I could find were those of Bourdot and Galzin for the widespread *Ganoderma applanatum*. I had reached the stage of plotting the theoretical curve for *Amauroderma* (Graph 13) when I realized this new possibility, and straightway found that the species-point for *Ganoderma applanatum* lay very near to the curve. Later, I was able to study living material of two species, *G. rivulosum* and another unidentified, and to obtain two new points (a species-point and an average point) which fitted almost exactly the backward extension of the *Amauroderma*-locus. As can be seen from Fig. 3, *Ganoderma* has the dumpy basidium of *Amauroderma*, though being smaller it is less strikingly clavate or pyriform, and the fact that both conform to the same locus on the basidiograph proves that they are related genera with the same kind of basidium. The fact, also, dispelled any misgiving that the species-point could be relied on, for it was not until I saw such a point on paper that I troubled to look at *Ganoderma*-basidia and perceived the art of nature.

Developing basidia. Just as with spores, it would seem that the backward extension of the locus on the basidiograph should represent the development of that kind of basidium.

* This 'species c' is *Mycena illuminans* P. Henn. and *M. bambusa* Kobayashi. The combination under *Oudemansiella*, which is a very vaguely understood genus because of its unknown tropical ramifications, has not been made. Species 'b' and 'a' are less closely related and may be a distinct genus.

I tried to get data for some species of *Clavaria* but failed, for the reasons already given; no doubt suitable species will be discovered, but in those that I examined it was impossible to extricate the young basidia without crushing or injuring them, and most were curved. I found the large basidia of *Oudemansiella Canarii*, with very short stalk, suitable and

Table 14. Average data for the length (*l*) and width (*w*) of developing and mature basidia of *Oudemansiella Canarii*

Data according to increasing values of *l* (*l*-order)

<i>l</i>	<i>w</i>	<i>l/w</i>	Range of <i>l</i>	Range of <i>w</i>	Range of <i>l/w</i>	No. of basidia
7.7	4.5	1.72	—	—	—	1
13.63	5.53	2.47	13.5-13.8	4.6- 6.5	2.08-3.02	2
18.25	5.73	3.19	18-18.5	5.7- 5.8	—	2
21.88	6.97	3.14	21.3-22.4	6.0- 8.0	2.66-3.67	3
26.75	9.68	2.76	25.8-28.5	7.3-14.0	2.04-3.70	6
32.21	10.33	3.12	30.5-34.8	7.0-12.9	2.43-4.82	7
37.46	11.35	3.30	36.0-39.8	9.6-12.7	2.82-4.08	7
42.43	13.94	3.04	40.3-44.8	11.6-16.1	2.72-3.84	13
47.13	15.53	3.03	45.0-49.5	12.3-17.5	2.69-3.88	18
53.21	17.38	3.06	50.4-56.0	13.7-20.0	2.44-3.98	11
63.87	19.78	3.23	60.5-69.0	16.5-22.1	2.82-3.88	8
74.06	20.22	3.66	72.5-77.0	18.0-23.0	3.22-4.03	8
81.8	25.5	3.21	—	—	—	1
55.5*	20.20	2.75	53.0-59.0	18.5-21.5	2.47-3.19	3
67.0*	21.94	3.05	64.0-69.0	21.0-22.5	3.00-3.10	4
74.1*	23.64	3.13	70.0-77.5	21.0-25.3	2.83-3.36	7
81.14*	24.34	3.33	80.0-83.5	21.0-27.4	2.92-3.84	7
92.75*	23.93	3.88	90.0-95.5	20.3-27.6	3.46-4.45	2
(Av. 74.20*)	23.40	3.21	53.0-95.5	18.5-27.6	2.47-4.45	23)

* Full-grown basidia without spores.

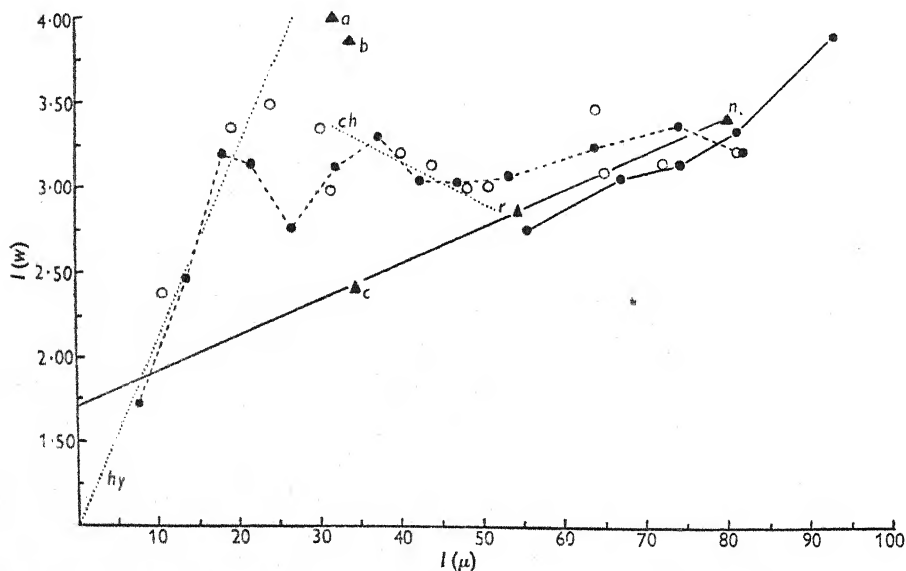
Data according to increasing values of *w* (*w*-order)

<i>w</i>	<i>l</i>	<i>l/w</i>	Range of <i>l</i>	Range of <i>w</i>	No. of basidia
4.53	10.75	2.38	7.8-13.8	4.5- 4.6	2
5.82	19.50	3.35	18.0-22.0	5.5- 6.0	3
6.91	24.10	3.49	13.5-33.5	6.5- 7.3	4
9.04	30.25	3.35	21.3-49.8	8.0- 9.8	8
10.55	31.44	2.98	25.8-36.0	10.0-11.0	4
12.53	40.08	3.20	30.8-47.5	12.0-13.3	13
14.05	43.92	3.13	28.5-54.5	13.6-14.5	12
16.08	48.18	3.00	43.5-56.0	15.5-16.4	11
16.96	50.78	3.00	45.8-64.0	16.5-17.4	8
18.50	63.90	3.46	54.0-74.5	18.0-19.4	10
20.98	64.90	3.09	51.5-77.0	20.0-21.6	12
23.04	72.0	3.13	—	—	1
25.5	81.8	3.20	—	—	1
18.5*	59.0	3.19	—	—	1
21.14*	67.00	3.17	53.0-90.0	20.3-21.8	6
22.70*	73.00	3.22	67.5-83.0	22.5-23.0	7
24.50*	76.04	3.10	70.0-80.0	24.0-25.3	5
27.00*	84.25	3.13	80.0-95.5	26.0-27.6	4

* Full-grown basidia without spores.

accordingly studied them in detail. The data for eighty-nine developing basidia and twenty-three full-grown basidia are given in Table 14, according to two arrangements. The measurements were taken from camera lucida drawings (necessary for other measurements which cannot be made satisfactorily on living specimens). Examination of young

basidia in the same stage of development, as indicated by their contents, showed that they vary greatly in length for a given width, and vice versa. Neither length nor width is, therefore, a good criterion of the state of development. A third measure, which is the perpendicular distance from the apex of the basidium to the plane of w , seems to give a truer measure of development, but I do not wish to digress more than necessary to show that one is on the edge of a new field of enquiry, and that general principles must come before the explanation of aberrations. My conclusion is that no linear measure of the basidium is an absolute index of its state of growth. Basidia arise at various depths in the subhymenium and enlarge toward the surface, or hymenial level, where, as nearly full-sized cells, they form a palisade; then they protrude beyond this level to maturity as



Graph 12. Basidiograph of developing and mature basidia of *Oudemansiella Canarii* and its allies (ref. Tables 13, 14). Continuous lines are the loci for mature basidia; that for species-points (triangles) corresponds with the locus *O* in Graph 11: that connecting the average points (circles) is based on the separate data of Table 14. Dashed lines connect the points for the developing basidia of *O. Canarii*, according to the l -order of Table 14. The empty circles give the points for the w -order of Table 14. Dotted lines: *hy* is the inferred locus for the young basidia of *O. Canarii* up to $25\ \mu$ long; *ch* is the inferred locus for the half-grown basidia 32 – $52\ \mu$ long. Species-points: *a*, *Oudemansiella* sp. *a*; *b*, *Oudemansiella* sp. *b*; *c*, *Oudemansiella* sp. *c*; *n*, *O. canarii*; *r*, *O. radicata*.

mono-, di-, tri-, and tetramorphic basidia in Buller's sense. The base-line from which measurements must be taken to indicate the state of growth is the hymenial level. Distances from this level to the tip of the immersed basidium will indicate inversely the early stages of development, and distances outward will indicate directly the later stages. The problem is to find this level and, in the same section, basidia which are measurable. I have not been able to overcome the practical difficulties and, therefore, have taken two orders to indicate the change in shape as the basidium grows.

The resulting basidiograph (Graph 12) is complicated and its analysis takes one to the next step of studying the basidium as a whole, but I must defer this to a later paper. Nevertheless, certain features can readily be understood if one assumes that the ideal locus is a straight line.

The data for both l - and w -orders indicate a peak when the basidium is $25\text{--}30\mu$ long. Up to this peak the basidia develop as narrowly clavate, *Clavaria*-like basidia which elongate much more rapidly than they widen. After the peak, the ratio alters and the basidium widens more rapidly than it lengthens. A second inflexion occurs about the region when the basidium is 55μ long, which is the minimum length of mature basidia. After this inflexion the mature basidia conform with the *Oudemansiella*-locus already established (c - r - n in Graph 12). The first phase, shown by the dotted line hy , is that of hypha-like upgrowth at the base of the hymenium. The second phase, shown by the dotted line ch , is that of widening while the basidium fills up with the dense cytoplasm to be injected into the spores; I call this the stage of charging the basidium. The third phase is that of accommodation of the apex of the basidium on the hymenium without interference with neighbouring basidia. Thus this curve of growth can be analysed into three straight lines arranged like an inclined **Z**, and it is probable that the basidiographs of all developing basidia will have this shape to some extent.

Now the remarkable fact emerges that of the three species a , b , and c , with basidia about the same length, c fits the locus of the mature basidia of the genus, whereas a and b , at first sight so aberrant (Graph 11), fit the initial *Clavaria*-like locus of the developing basidium. Clearly, one has penetrated deeply into the mechanism of the basidium by this simple graphic method, and discovered how one kind of basidium may be related to another; how the *Clavaria*-basidium corresponds with the very young basidium of *Oudemansiella*.

GENERAL RELATION BETWEEN LENGTH AND WIDTH

Basidia. Taking, as the equation for a straight line, $y = a + bx$, for the basidiograph-locus one can write

$$\frac{l}{w} = a + bl,$$

whence

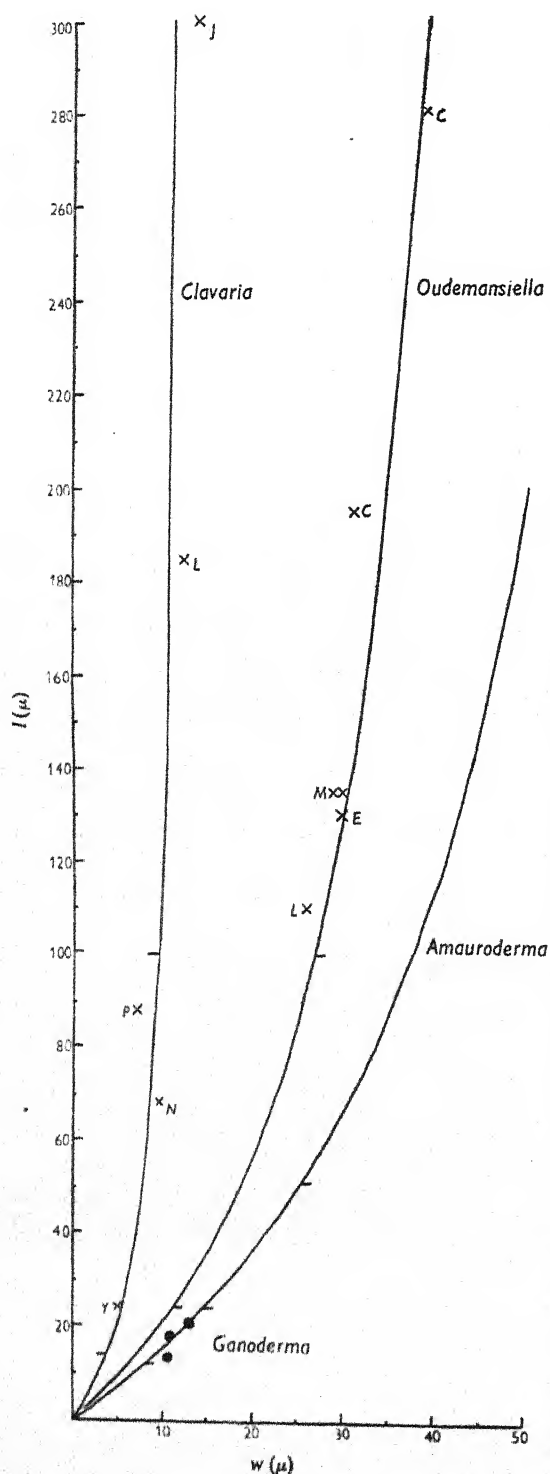
$$l = \frac{aw}{l - bw} \quad \text{and} \quad w = \frac{l}{a + bl}.$$

A series of such curves relating l and w are shown in Graph 14. They are rectangular hyperbolas for which w is asymptotic to a value given by the reciprocal of b (or by the cotangent to the basidiograph-locus). From the point of view of the basidium, the peculiarity of the curve is that, while the length may increase indefinitely by apical growth, the width soon approaches a limit. Thus, as already observed, length varies much for little change in width. The slope of the basidiograph varies inversely with the maximum width, a steep slope giving a narrow basidium.

From the loci inferred from the data in Tables 12-14, the following values can be given to the constants for the three kinds of basidium:

	Value of a	Value of b	Limit of w
<i>Clavaria</i> -basidium	2.60	0.08	12.5μ
<i>Oudemansiella</i> -basidium	1.70	0.02	50.0μ
<i>Amauroderma</i> -basidium	1.35	0.013	77.0μ
Developing basidia of <i>Oudemansiella Canarii</i> :			
First phase, to 27μ long	1.00	0.11	
Second phase, $32\text{--}52\mu$ long	3.90	-0.02	

Among the Clavarioid fungi which I have considered, none has a basidium exceeding 12.5μ wide as a mean or average value; most have w less than 10μ , and the few



exceptions, up to 13μ wide, may have been compressed basidia. Theoretically, a *Clavaria*-basidium 12.0μ wide should be about 8000μ long. The basidia of *C. pistillaris* are the longest in the group, being $90-120 \times 11-13\mu$, but there is good reason to believe that its basidia belong to a different kind, that of *Cantharellus*, which has a smaller value for b ; hence I have omitted it, and its allies, from the data in Table 12.

There are certainly no basidia of *Oudemansiella* and *Amauroderma* approaching their limits. Theoretically, a basidium 40μ wide would in each case be, respectively, 340 and 113μ long, and such enormous basidia are not known.*

In Graph 13, the curves relating l and w for the three kinds of basidium are drawn through points calculated from their equations. The parts of the curves which concern the basidia are below the steepenings of the curves towards their limits.† The

* Such asci are known, and if, as seems likely, the ascus can be analysed in the same way as the basidium (though not, of course, the endogenous ascospore), some light will certainly be thrown on the different mechanisms of the two reproductive cells.

† I could find no accurate measurements of w for *Oudemansiella mucida* and *O. longipes*. Bresadola gives $50-70 \times 10-15\mu$ for *O. mucida* (*l.c. Myc.* t. 600): Ricken gives $50-60 \times 14-16\mu$: both authors give the spores as $14-18\mu$ wide, and thus wider than the basidium which cannot be true. Similarly for *O. longipes*, with basidia $45-50 \times 7-8\mu$ (Bres.), $36-40 \times 8-10\mu$ (Ricken). Assuming that l is 55 and 38μ respectively, w will be 19.9 and 15.5μ .

Legend for Graph 13.

Graph 13. Curves relating length (l) and width (w) for the basidia of *Clavaria*, *Oudemansiella*, and *Amauroderma*. The horizontal marks on the curves show the known limits of the basidia. The points of *Ganoderma* are shown as three black circles. Crosses mark the points for the cystidia of *Clavaria candelabrum* (J), *C. Leveillei* (L), *C. nebulosoides* (N), *C. purpurea* (P), *C. pyxidata* (Y), *Oudemansiella Canarii* (C), *O. echinosperma* (E), *O. longipes* (L), *O. mucida* and *O. radicata* (M). (Note, the horizontal scale is double the vertical.)

shapes of the curves describe the shapes of the basidia which may be regarded as hyperboloids of revolution topped by a semi-ellipsoid or hemispheric apex.

With regard to the constant a , which gives the value of the ratio $l:w$ when l is zero, it is the factor which cuts the capacity of the basidium by delaying the approach of w to its limit. A high value of a means a very gradual expansion of the cell as it grows apically. Short and wide basidia, as in *Amauroderma*, have low values of both a and b ; long narrow basidia will have relatively high values for each. The constant b will lie between 0.3 and 0.01 for subcylindric and clavate basidia.

Equation to the hypha. It is usual to regard the hypha as a cylindric vegetative filament of different category from the short, broad, reproductive basidium. But as a filament increasing in length without widening, the uninflated hypha is the living embodiment of the curve of Graph 14 in which $a=b=1$. Hyphal growth and shape can be expressed in the same way as for the basidium and the hypha displays the essential of the limiting curve—that l shall be large compared with w . The so-called constant width of the hypha is its gradual approach to the limiting value of w . Hyphae are often a thousand times as long as wide and may be a hundred thousand times as long, as in rhizomorphs, though in such strands they usually branch and grow sympodially when more than a few centimetres long.

In Basidiomycetes, uninflated hyphae are mostly 1–5 μ wide. The value of b will therefore lie between 0.2 and 1.0. The value of a is less obvious but, as the hypha quickly attains its normal width, it must be low. Thus, for a 3 μ hypha, one may take $a=1$ and $b=0.33$, and then,

when l is	1 μ , w is 0.75 μ ,
when l is	5 μ , w is 1.88 μ ,
when l is	10 μ , w is 2.31 μ ,
when l is	50 μ , w is 2.83 μ ,
when l is	100 μ , w is 2.91 μ ,
when l is	1000 μ , w is 2.99 μ .

Therefore, unless the hypha was measured carefully during its initial growth of 30 μ , it would be described as 3 μ wide. A lower value of a , such as 0.1, gives the hypha as 2.83 μ wide when 5 μ long. Thus, a probably lies between 0.001 and 1 for the hypha. The characteristic period of growth of the hypha is its earliest stage on origin from a spore or parent hypha; when only 1–5 μ long, it may be wider than long; very quickly it reaches its maximum width.

To test the deduction, I measured the length and width of the germ tubes in Buller's drawings of the germinating spores of *Coprinus sterquilinus* (1931, fig. 51) and *Pyronema domestica* (1933, fig. 62b). By plotting the ratio $l:w$ against l , as a hyphagraph, and drawing a mean locus, I obtained the following values:

Hyphae of <i>C. sterquilinus</i> :	$a=0.30$, $b=0.116$, limit of w 8.60 μ ;
Hyphae of <i>P. domestica</i> :	$a=0.35$, $b=0.155$, limit of w 6.45 μ .

These limits agree with the average width of the mycelial hyphae in these species, e.g. 7 μ for *Pyronema domestica* (as in Buller's fig. 63, 1933).

From the change in shape of the germ tube, one can arrive at the equation to the

hypha. Without this equation one cannot understand the transformation which produces the basidium from the hypha. Without both equations one cannot understand the partition of the basidium unit into a tetrad of subparallel spores which reproduce the hyphae. Comparison of the cycle of data in related species and genera should enable one to penetrate far into the problems of microscopic size and form.*

There are, of course, complications caused by the inflation of the hyphae, and it seems that a must be greater than unity in some cases where the maximum width of the hypha is attained very gradually, as in skeletal hyphae which dilate over stretches of 100–1000 μ from 2 to 6 μ wide.

Equations to basidia. (1) When $a=1.5$, $b=0.15$, limit of $w=7.0 \mu$. This roughly describes the long, narrow, subcylindric basidium of the Auriculariaceae, in which the variation in length is 20–300 μ and in width 4–7 μ . It is the most hypha-like basidium with least capacity, and it corresponds with the first phase in the developing basidium of *Oudemansiella*. Transverse septation, as in a hypha, seems the only way of discharging a tetrad of spores, as the apex of the basidium is too small to accommodate a circle of spores, and there is no compact charging. The basidium of the Dacryomycetaceae must be similar, but it is able to accommodate the two sterigmata at the apex.

(2) When $a=1.2-3.5$, $b=0.05-0.08$, limit of $w=12-20 \mu$. This describes the narrowly clavate *Clavaria* basidium which is suited to the thickening hymenium, and it probably describes also the Cantherelloid and many Stereoid basidia. It is never so hypha-like as the *Auricularia* basidium. It has long-delayed and comparatively slight, subapical, charging which provides the platform for the spore circle. Having a limited capacity, it does not produce large spores. It is intermediate in shape and mechanism between the *Auricularia* and the *Oudemansiella* basidium.

(3) When $a=1.5-3.0$, $b=0.02-0.05$, limit of $w=20-50 \mu$. This describes the broadly clavate, or barrel-shaped, basidia of many agarics, as *Oudemansiella*, *Coprinus*, *Panaeolus*, *Amanita*, *Russula* and so on. It is the kind of basidium which builds the regular palisade layer of the unthickened hymenium so characteristic of these genera.

(4) When $a=1.35$, $b=0.013$, limit of $w=77 \mu$. This is the *Amauroderma* basidium which is the broadest in the Homobasidiomycetes, having the ratio $l=1.5-2 w$. It has the greatest capacity of all homobasidia, but little is known about it apart from its occurrence in the two genera *Amauroderma* and *Ganoderma*. In shortening the preliminary hyphal stage of the *Oudemansiella* basidium, it is the antithesis of the *Clavaria* basidium and, thus, it leads to the next kind.

(5) When $a=1$, $b=0$, $l=w$. This is the Tremellaceous basidium which inflates directly from a hyphal end into the globose or subglobose shape. It has, theoretically, the greatest capacity of all basidia but it does not seem to reach the size of either *Amauroderma* or *Oudemansiella* basidia. It is charged directly with dense protoplasm, without a preliminary hyphal stage, thus it is the counterpart of the *Auricularia* basidium. Cruciate septation seems the only way of producing the tetrad of spores. The Tremella-basidium, thus, differs more from the *Auricularia* basidium than it does from the *Amauroderma* basidium and it is difficult to see what close affinity can exist between these two groups of Heterobasidiomycetes.

* Even though ascospores may not have the same manner of growth, yet they give rise to hyphae which ultimately produce asci and, thus, there may be some interesting discoveries to be made in relating the equations for hyphae, asci and ascospores.

Equations to spores. For the sporograph locus

$$\frac{D}{d} = E = a + bD$$

and

$$a = E - bD \quad \text{and} \quad b = \frac{E - a}{D}.$$

From the loci inferred from the data in Tables I-II, values can be given to the two constants as shown in Table 15.

Table 15. Constants for the equations to basidiospores

	<i>a</i>	<i>b</i>	Limit of <i>d</i>	Range of <i>d</i>	<i>n</i> *
<i>Clavaria aurea</i>	0.745	0.146	6.87	3.0-6.0†	4
<i>C. botrytis</i>	0.483	0.167	6.00	4.5-5.5†	4
<i>C. flava</i>	0.600	0.150	6.67	4.0-6.5†	4
<i>C. formosa</i>	0.673	0.147	6.80	3.5-6.7†	4
<i>C. fragillima</i>	0.836	0.107	9.34	4.7-7.5	(1-) 4
<i>C. cyanocephala</i>	0.491	0.092	10.91	5.5-10.0†	2
<i>C. acuta</i> , and <i>C. Gibbsiae</i>	0.490	0.097	10.31	5.0-8.5	(2-) 4
<i>C. fumosa</i> and <i>C. purpurea</i>	1.024	0.118	8.48	3.0-5.0	4
<i>C. incarnata</i>	1.316	0.040	25.00	3.5-6.5	4
<i>C. fusiformis</i>	1.12	—	∞	6.0-8.5	4
<i>C. rugosa</i>	0.61	0.057	17.54	7.0-10.0	2
<i>C. pistillaris</i>	0.68	0.078	12.82	5.0-10.0	4
<i>C. juncea</i>	0.51	0.173	5.78	3.0-5.0†	4
<i>Typhula phacorrhiza</i>	1.272	0.071	14.08	4.0-8.0	(2-) 4
<i>T. hyalina</i>	0.883	0.116	8.62	4.0-5.7	2
<i>T. hyalina</i>	0.906	0.092	10.87	5.0-7.0	1
<i>Boletus funerarius</i>	1.480	0.055	18.18	5.0-6.5	4
<i>Hygrophorus firmus</i> macrospores	0.760	0.071	14.08	7.0-11.0	4
<i>Hygrophorus firmus</i> microspores	0.230	0.227	4.41	3.0-4.5†	4

* The number of spores per basidium. † Approaching the limiting width.

From this table one sees that spores resemble basidia rather than hyphae in being short and, generally, below their limiting widths; yet, as with hyphae, *a* is low and the spore rapidly widens. Where *a* is less than unity, the spore rudiments are probably broader than long, but it is also likely that the parts of the species-locus below the base-line (where *E* is unity) are unreal, and that up to its intersection with the base-line the spores are subglobose.*

In *Clavaria cyanocephala* and *C. pistillaris* some spores slightly exceed the theoretical limiting width; they may be abnormal or derived from basidia with fewer sterigmata than usual.

There are, however, relations between *d* and *w* and between the volume of the spore and that of the basidium which must be analysed before one can relate the spore equation with that of the basidium.

* The sporographs of *Clavaria juncea*, *C. pistillaris* and *C. rugosa* indicate globose spores when *D* is 3, 4 and 7 μ respectively. Subglobose spores do not occur in the alliance of the first two species where the spores of all related species are rather large, those of *C. juncea* being the smallest. But, in the alliance of *C. rugosa*, there are several species with subglobose spores 6-8 μ long, as *C. cinerea*, *C. cristata* and a number of tropical species.

CYSTIDIA

In spite of many attempts to classify and homologize cystidia, it is still generally overlooked that (1) cystidia are characteristically the first hymenial elements to mature, being derived from the first hyphal endings in the primordial hymenium; (2) later developed cystidia commonly have transitions to the basidia with which in time and place of development they agree.

It seems that cystidia represent sterile basidia which become overgrown without charging. If so, they should conform with the basidiograph locus for the species or genus. I have no data to construct a cystidiograph, but in Table 16 I have given the size of the

Table 16. *Size of cystidia*

Species	Observed size (μ)		Calculated width (μ) for	
	Range	Mean	Mean length	Max. length
<i>Clavaria nebulosoides</i>	65-70 \times 7-12	68 \times 9.5	8.4	8.5
<i>C. purpurea</i>	45-130 \times 5-9	88 \times 7.0	9.2	10.0
<i>C. cystidiophora</i>	50-70 \times 5-8	60 \times 6.5	8.0	8.5
<i>C. luteicola</i>	16-18 \times 5-6	17 \times 5.5	4.3	4.4
<i>C. Léveilléi</i> *	70-300 \times 10-15	185 \times 12.5	10.6	11.3
<i>C. candelabrum</i> *	—600 \times 8-20	300 \times 14.0	16.0	18.0
<i>C. pyxidata</i>	18-30 \times 4-6	24 \times 5.0	5.1	6.0
<i>Typhula hyalina</i> *	40-90 \times 5-12	65 \times 8.5	9.7	11.3
<i>T. hyalina</i> var.*	30-50 \times 5.7	40 \times 6.0	7.5	8.5
<i>Perona Montagnei</i>	—	23 \times 5.5	5.2	—
<i>Oudemansiella Canarii</i> *	110-280 \times 23-40	195 \times 31.5	35.0	39.7
<i>O. longipes</i> †	80-140 \times 20-32	110 \times 26.0	28.2	31.1
<i>O. mucida</i> ‡	90-180 \times 15-45	135 \times 30.0	30.7	34.0
<i>O. radicata</i> ‡	110-160 \times 16-42	135 \times 29.0	30.7	32.7
<i>O. echinosperma</i> §	100-160 \times 9.5-30	130 \times 30	30.2	32.7

* My measurements: those of *C. javanica* being for gloeocystidia.

† Konrad & Maublanc, *lc. Sel. Fung.* t. 199, t. 217.

‡ Rea, *Trans. Brit. Mycol. Soc.* 12, 1927, 209.

§ Singer, *Mycol.* 37, 1945, 439: 'mostly 128-130 \times 28-30.'

cystidia in some *Clavarias* and in some species of *Oudemansiella*, together with the theoretical values for w as calculated from their basidial equations. Unfortunately, cystidia rarely occur in *Clavaria* and I have taken most data from other authors. The observed and calculated figures agree well enough for one to assume, as a working hypothesis, that cystidia conform to the same equations as the basidia. Certainly this must be true for *Oudemansiella* which has very large cystidia, easy to measure, and for which the independent data of four authors agree so closely with the calculated values. For *Clavaria candelabrum*, *C. pyxidata* and *Typhula hyalina*, I have used the equation to the basidia of *Clavaria pistillaris* and its allies, for they possess a relatively wider basidium than typical of other *Clavaria* (having $a=3.4$, $b=0.05$). Thus, very remarkably, the long subhymenial gloeocystidia of *C. candelabrum*, which traverse its thickened hymenium (as these organs do in the *Gloeocystidium* section of *Corticium*), conform to the same equation as do the short hymenial cystidia of *Clavaria pyxidata*; both species are closely related and widely different from most *Clavarias* in microscopic construction.

I conclude that cystidia develop in the same way as the basidia but, through precocity or sterility, they become overgrown and much larger than the basidia. For lack of material, they may be unable to maintain the great diameter which, theoretically, they should develop and, therefore, they become attenuate and ventricose or lanceolate instead of progressively clavate. The cystidium of *Clavaria Léveilléi* (Fig. 4a), however, maintains its great diameter.

The conclusion is important because in many genera the basidia differ so little in size that it may be impossible to obtain an accurate basidiograph. The cystidia, if present, will then supply the higher values of l ; for example, *Mycena*, *Pluteus*, *Inocybe*, *Psathyra*, *Coprinus*, *Hymenochaete* and so on.

LENGTH : WIDTH CURVES

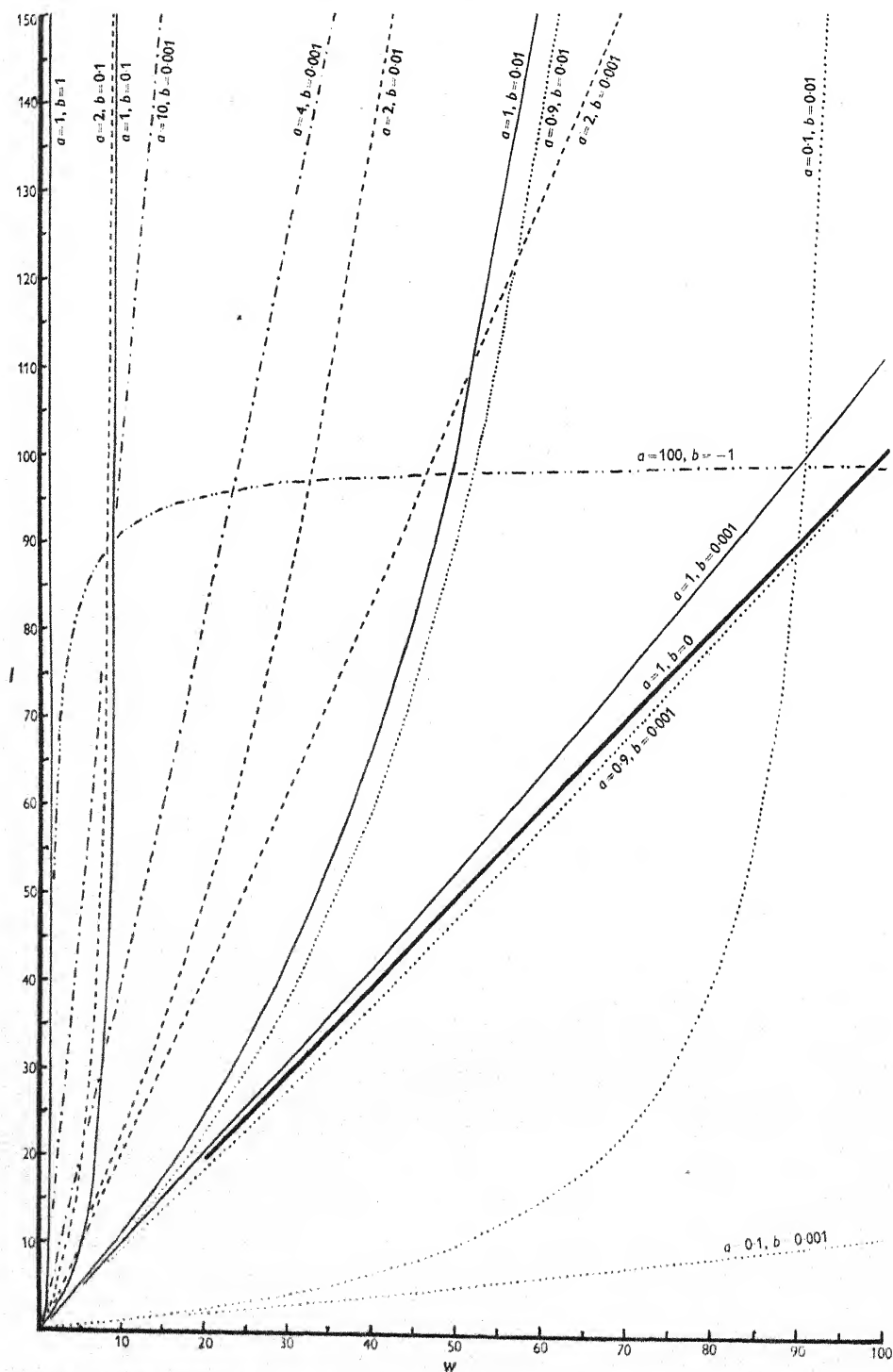
Morphological properties. If these curves are expressed conventionally as equations between x and y (instead of l and w), they will appear in graphs as tending to horizontal asymptotes. But, considered mycologically, they are morphological curves, and it is usual, as well as helpful to the eye, to orientate drawings of fungi, with the length vertical. I have, accordingly, in Graph 14, plotted l vertically instead of horizontally. It can be seen at once that the curves are the outlines which bound sections of fungi, macroscopically as well as microscopically.

Thus the curve ($a=1$, $b=1$) expresses a relation between l and w which implies very pronounced longitudinal growth. When

Fig. 4. Cystidia, with their basidia, mentioned in the text. a, *Clavaria Léveilléi*; b, *Typhula hyalina*; c, *Clavaria candelabrum*; d, *Oudemansiella Canarii*; $\times 500$.

revolved through 360° about the l -axis, it describes a 2μ hypha or a 2 mm. filiform fruit-body (as *Clavaria juncea*) or the stem of a *Mycena*. The curve ($a=2$, $b=0.1$) describes, on revolution, the narrowly clavate basidium and the similarly shaped *Clavaria* fruit-body. The wide-bellied curve ($a=0.1$, $b=0.01$) describes, on revolution, the base of the stem of agarics with massive primordia wider than long (as in *Amanita* or *Cortinarius* subgen. *Phlegmacium*) as well as the fruit-body of *Bovista* or *Scleroderma*; it has no microscopic counterpart because it is the frustration of apical growth.* The curve ($a=1$, $b=0.1$) describes, on revolution, the fruit-body of a *Solenia* (which,

* Possibly in the wide paraphyses of *Bolbitius* and *Coprinus*, as the last-formed hymenial elements with least apical growth.



Graph 14. Curves between l and w , for the equation $l = w(a + bl)$. Continuous lines for $a = 1, b = 1, 0.1, 0.01, 0.001$ and 0 . Dashed lines for $a = 2, b = 0.1, 0.01$ and 0.001 . Dot-dashed lines for $a = 4, b = 0.001$ and for $a = 10, b = 0.001$. Dotted lines for values of a less than unity.

however, is inverted). The almost rectilinear curves ($a=4$, 2 and 1, $b=0.001$) show the divergence of the limb of the pileus in *Stereum*, *Polyporus* and so on.

If b is negative, the relations between l and w are exchanged, l becoming limited by a horizontal asymptote given by the value of a/b (that is, when w is infinite, $a=bl$). The curve ($a=100$, $b=-1$) suggests the infundibuliform pileus and, with a higher value for a , will give the long cylindric stem sharply deflected at the apex to the horizontal centric pileus of *Amauroderma rugosum*.

I conclude that not only do hyphae individually possess hyperbolic, or asymptotic, growth, but that this peculiarity directs also their growth in tissues to form the fungous somata.

The constants a and b . The obvious feature of these curves, apart from their asymptotic character, is the tendency towards rectilinear relations between l and w when a is large compared with b ; the equations then become, practically, $l=aw$. A special case is the diagonal, $l=w$, approached as a tends to unity and b to zero; sets of such curves give, with decreasing values of b , a flattening along the diagonal.

A second feature of analytical, or morphological, importance is the close resemblance which may exist between curves of very different sets, at least near the origin. Thus, up to $l=40$, the three curves ($a=1$, $b=0.1$; $a=2$, $b=0.1$; $a=10$, $b=0.1$) would be almost impossible to distinguish directly from observational data and, below $l=20$, the confusion is greater. Thus, short and narrow organs or bodies have a superficial resemblance because they have no scope to develop and display their peculiarities, e.g. the $6 \times 3 \mu$ spore and the $25 \times 6 \mu$ basidium. Direct values, or $l:w$ curves, are useless for analysis, which is provided by the sporograph, basidiograph, etc. The straight lines of these graphs are the differentials of l with respect to w in the equation $l=w(a+bl)$, and they resolve a and b clearly into separate measures.

Meaning of the constants. If a juvenile protoplast, such as an immature basidiospore, grows as a sphere, its surface must increase uniformly by intussusception. Apical growth, as unidirectional enlargement, must be caused by the fixation of the surface-layer into a rigid wall except for a polar cap which continues to grow and protrudes. If the protrusion has a constant diameter, the rate of acropetal fixation of the new wall, developed from the polar cap, must be balanced by the rate of interstitial enlargement of this cap. If the rate of fixation increases relative to that of enlargement, the protrusion must taper to a point where it is entirely confined by a fixed or rigid wall. If, on the other hand, the rate of fixation decreases relatively, the polar cap (or hyphal tip) expands obconically. Such relative variations in the rates of apical growth and acropetal fixation of the wall will give a direct linear relation between the length, as the outcome of apical growth, and the width, as the outcome of apical enlargement or diminution: that is to say, if y is the rate of lengthening and x that of fixation, then w varies as $y:x$. Thus, the constant a seems to represent the relative rate of fixation of the wall. The constant b , which gives the maximum width attainable by the protrusion, must represent either the maximum width attainable by the polar cap or the maximum distension of the unfixed wall immediately behind the cap or apex. The process of fixation would appear to be the chitinization of this hemicellulose wall, whereas the limitation would appear to affect the immature hemicellulose part of the wall. Possibly filamentous algae, with different wall structure, will provide tests for deductions from fungous structures. Certainly one needs clearer analysis of the apical growth of expanding and contracting filaments.

CONCLUSION

This simple expression for the outcome of the intricate details of hyphal growth serves to open up many new problems. Some of these I have indicated and have been able to pursue with satisfaction; others are baffling. The cystidium of *Clavaria Léveilléi*, for instance, has, as one would expect, the gradually clavate form of the *Clavaria* basidium and fruit-body, but that of *Oudemansiella* is widest about the middle of its length where, theoretically, it should still be expanding. This level is the hymenium level for the maximum width of basidia and cystidia. One must conclude that the single-layered hymenium of agarics differs from the thickening hymenium of *Clavaria* in having an induced level. The evolution of gills and tubes, with which the single-layered hymenium is connected, must be related to the reorganization of the factors evoking the hymenium, and in this light one must trace the stages which have lead to the perfection of *Coprinus*, the sterility of *Nyctalis* and the disintegration of the hymenium in *Gasteromycetes*.

SUMMARY

Measurements of basidiospores show that there is a general relation between the length (D) and the width (d) which can be expressed as $D = d(a + bD)$. Spore-size and shape (indicated by the ratio $D:d$) in a species, or in a group of closely allied species, can be analysed graphically by plotting the ratio $D:d$ against D to obtain a straight line, the cotangent of which is the maximum width attainable by that kind of spore. Such a graph is called a sporograph and the locus for a species a species-line. Spores of closely allied species conform to the same locus. Spores of different kinds have different loci defined by the values of the constants a and b . Examples are given from *Clavaria*, *Typhula*, *Boletus* and *Hygrophorus*.

A study of the data for length and width in the basidia of *Clavaria*, *Oudemansiella* (= *Collybia* pr.p.), *Amauroderma* and *Ganoderma* show that the same relation holds for the basidium. Generic, and family, kinds of basidia can be analysed in the same way by means of the basidiograph, and defined by the constants a and b .

The cystidia of *Clavaria* and *Oudemansiella* conform to the same equations as their basidia and are to be regarded as sterile, and mostly precocious and overgrown basidia.

This relation between length and width expresses the characteristic of hyphal growth as hyperbolic elongation to a limiting width. Curves of this kind, relating length and width, are morphological expressions of fungi, microscopic as well as macroscopic.

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STUDIES IN BRITISH PRIMULAS

I. HYBRIDIZATION BETWEEN PRIMROSE AND OXLIP
(*PRIMULA VULGARIS* HUDS. AND *P. ELATIOR* SCHREB.)

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(With Plate 5 and 4 figures in the Text)

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I. INTRODUCTION

In considering the relations between allied plant species two questions are bound to arise, first, how the species came into being as distinct entities in the course of evolution, and secondly, how the species are isolated from one another so that they remain distinct. This paper is to some extent concerned with both of these questions, but most directly with the second. As has been pointed out by Dobzhansky (1937), isolating factors may be of various kinds, e.g. ecological, geographical, cytological or genetical; their relative importance can best be assessed by combining experimental investigations on interspecific hybridization and observation on populations of the species under natural conditions. One of the few investigations of this type which has been made on members of the British flora is that of Marsden-Jones & Turrill (1928-40) on *Silene maritima* and *S. vulgaris*; a summarized account is given by Turrill (1946). But, as Baker (1945) has indicated, there are probably many interspecific hybrids yet to be recognized in Great Britain alone; and there is very much work to be done on the fairly large number of well-known hybrids.

The work to be described here deals with the Primrose, *Primula vulgaris* Huds., and the Oxlip, *P. elatior* Schreb. As was first shown by Christy (1897), the Oxlip is confined in Britain to a small area in East Anglia, and at the edges of this area Oxlip-Primrose hybrid populations are found; such well-defined hybrid swarms are not common amongst British plants. Work was begun in 1937 with the object of investigating further the factors which determine the distribution of the species, and in particular the part played by hybridization in affecting this distribution. The work was completely interrupted by the war, but it has recently been restarted, and sufficient data are now available for an account to be given.

The present paper deals with the hybridization experiments; the bearing of these on the situation in the field will be considered in a subsequent paper.

II. DESCRIPTION OF THE SPECIES

The following descriptions are taken from Babington (1922). Both species are hemi-cryptophytes of the rosette type.

P. vulgaris Huds. *Leaves* oblong-ovate, tapering downwards, wrinkled, crenate, *young leaves* reticulate-rugose, *scape* rudimentary, *peduncles* villose, radical, one-flowered, *flowers* erect, *calyx* tubular, villose, teeth lanceolate-subulate, very acute, *corolla limb* flat, with a circle of scale-like folds at the slightly contracted mouth, *capsule* ovate, half the length of the calyx, long straightish teeth of *fruiting calyx* meeting at top, *fruit* nodding.

P. elatior Schreb. *Leaves* ovate, abruptly contracted below, then attenuate, wrinkled, denticulate, *young leaves* transversely plicate, *scape* umbellate, many-flowered, outer *flowers* nodding, *calyx* tubular, teeth lanceolate acute, *corolla segments* almost square, *corolla limb* concave, segments obcordate-oblong, its tube not crowned nor contracted at the mouth, *capsule* linear-oblong, exceeding calyx, teeth of *fruiting calyx* patent, fruit erect.

III. MATERIAL AND METHODS

Potted plants grown in a cool greenhouse have been used. With long-styled 'pin' female parents, emasculation has in general been found to be unnecessary, the plants being screened with a cage to prevent visits of insects, though insects have rarely been observed in the greenhouse. With short-styled 'thrum' female parents, the corolla, corolla-tube and stamens have been cut off the flower at an early stage, some days prior to pollination; flowers emasculated in this way have usually set seed normally after artificial pollination.

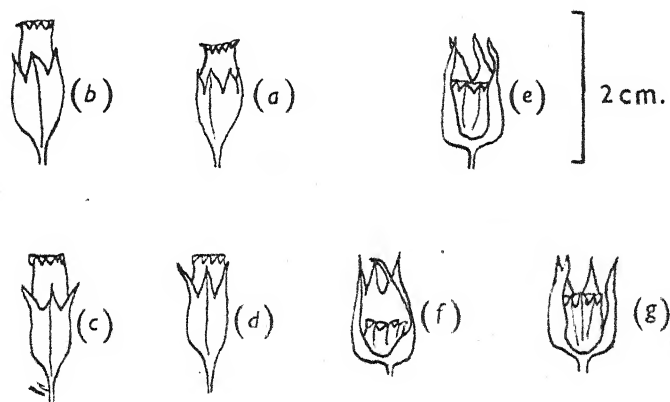
The experiments fall into two series, the first being done in the period 1937-40, the second in 1946. In both periods the plants selected for crossing were usually taken from pure populations of Oxlip or Primrose, i.e. in order to eliminate the possibility of selecting hybrid stock, they were not taken from woods in which both species grew. In the first period, the stocks of Primrose and Oxlip were both exclusively East Anglian, and came from a considerable number of boulder-clay woods either in or adjoining the Oxlip area.* In the second period, the Oxlips used were, of necessity, East Anglian, but the Primroses were taken from a wood in the north of England near Durham; this was an oak wood on a non-calcareous sandy loam of glacial origin.

The time from pollination to setting of ripe seed is two months, or slightly more. The course of events differs in the two species. In the Primrose, after a legitimate cross ('pin' \times 'thrum', or vice versa), the stigma and corolla wither, usually within a week, and the ovary then begins to swell. At the same time the calyx increases both in length and breadth. The fruit stalk remains in roughly the same position as when the flower was open, i.e. ascending or horizontal, or it may be deflexed down to the soil. Eventually the fruit dehisces, the teeth at the apex bending back, and the seeds are exposed; at this stage the fruit stalk may still be green and fresh. The relative proportions of calyx and fruit are indicated in Text-fig. 1 e. The length of the capsule and the condition of the seeds depends on the male parent; if this was a Primrose, the seeds are plump and black, and they adhere

* The Primroses used came from Park Wood, Elmdon, Essex, and Little Paxton and Brampton Woods, Hunts. The Oxlips came from Hayley, Langley, and Little Widgham Woods, Cambs, and from Spriggs Wood, Essex.

to the placenta and each other by means of a gummy substance which is secreted in some quantity by the placenta. The seeds thus cannot fall out of the capsule; they remain till the capsule rots away or until they are removed. The gummy substance is attractive to ants, which collect the seeds from the capsules, and so aid in dispersal (Sernander, 1906). If the male parent was an Oxlip, the seeds may or may not be sticky. If not sticky they are usually small and lie loose in the capsule. Data on variation in seed and capsule size in the cross Primrose ♀ × Oxlip ♂ are given in Table 3.

The course of events after pollination of the Oxlip flower is at first similar to that in the Primrose, viz. withering of the stigma and the corolla. The Oxlip flowers are in a drooping position at the top of a peduncle; a week or two after successful pollination, they erect themselves into a vertical position, in which they remain. The calyx increases slightly in length and considerably in breadth, and is soon considerably exceeded by the ripening capsule, which eventually dehisces, the teeth curling back at the apex (Text-fig. 1*a*). The



Text-fig. 1. Sketches of ripe, dry fruits. Name of seed parent given first. (a) Oxlip × Oxlip, 1946. (b) Oxlip ♀ × Primrose ♂, 1946. (c) and (d) F_1 hybrid ♀ × Primrose ♂, 1939. (e) Primrose × Primrose, 1946. (f) Primrose ♀ × Oxlip ♂ (cross, 1946*b*, Table 8). (g) Primrose ♀ × Oxlip ♂ (cross, 1946*c*, Table 8).

ripe seeds lie loose in the capsule, whose stalk is withered by the time it is ripe and open. Drops of fluid are often noted inside the top of the unopened capsule, and it is not until these have slowly evaporated that the capsule opens. There is no stickiness on the seeds, whatever the male parent of the cross, though, as also noted by de Vries (1919), there is in the interspecific cross a slight tendency for the seeds to adhere to the placenta even when fully ripe, rather than lie loose in the capsule as in the intraspecific cross.

The crosses described in the tables below are all 'legitimate', i.e. pin × thrum or vice versa. Three 'illegitimate' interspecific crosses (pin × pin or thrum × thrum) involving ten pollinated flowers, were made. Nine pollinations did not take, and the tenth, with Oxlip as female parent, gave a few large seeds which probably contained no embryo.

A few plants were selfed, but no systematic investigation of the effect of selfing was made; two Primroses selfed (three pollinated flowers) set a few apparently good seeds, and three Oxlips selfed (ten pollinated flowers) set only a very few seeds, from which, however, two seedlings were obtained.

IV. EXPERIMENTAL DATA

Much work has been done in artificial hybridization between members of the Vernaes section of the genus *Primula*, particularly on the Primrose and the Cowslip (*P. veris* L.). Darwin (1892) refers to a cross which he made between Primrose and Oxlip, and compares the seed production with that of a cross between Primrose and the Primrose-Cowslip hybrid. More recently, an extensive series of crosses was made by Eva de Vries (1919), and her data will be reviewed here as will also those of Heslop Harrison (1931). Melville (1936) has briefly reported experiments which demonstrate the fertility of the Primrose-Oxlip hybrid.

(a) *Production of fruit*

The results are set out in Table 1. For the same type of cross, pin ♀ × thrum ♂, and thrum ♀ × pin ♂ gave approximately the same result, and these are therefore not separated in the table. The few results available for intraspecific crosses are given here for comparison with the interspecific crosses.

In a few cases where Primrose was female parent, ripening fruits went mouldy and died before completing their development; such fruits are included in the column 'fruits produced'.

The data of de Vries (1919) are set out in Table 2 for comparison. de Vries worked with central European material, and the plants, from wild habitats, were grown out of doors and pollinated in an experimental garden.

Table 1. *Production of fruit in Primrose-Oxlip crosses*

Type of cross	Year	No. of ♂ parents used	No. of ♀ parents used	Total no. of crosses	Total no. of pollinations	Total no. of fruits produced	No. of fruits per pollination %
Primrose ♀ × Oxlip ♂	1937-40 1946	10 4	9 11	13 11	48 62	44 55	90
Primrose × Primrose	(1938 1946	3 3	3 3	3 3	14	13	93
Oxlip ♀ × Primrose ♂	1937-9 1946	3 4	9 5	10 5	40 29	40 28	98.5
Oxlip × Oxlip	(1938-9 1946	4 4	4 4	6 6	16	15	94

Table 2. *de Vries's data on production of fruit in Primrose-Oxlip crosses*

Type of cross	Total no. of pollinations	Total no. of fruits produced	No. of fruits per pollination %
Primrose ♀ × Oxlip ♂	388	172	51
Primrose × Primrose	142	104	73
Oxlip ♀ × Primrose ♂	509	248	49
Oxlip × Oxlip	167	129	77

From our data in Table 1, it may be concluded that the percentage of fruits set in both inter- and intraspecific crosses is very high and that there is little difference in this respect between the four crosses listed. Fruit production is lower in all de Vries's crosses, and

this may perhaps be ascribed to occasional unfavourable conditions in the garden in which she worked; there is, however, in her data, a marked difference between the inter- and intraspecific crosses which appears to be significant, and we may conclude that this marks a real difference between her material and ours, indicating a lower interspecific compatibility in the central European material than in the British.

As already mentioned above, the size of the capsules produced in the cross *Primrose* ♀ × *Oxlip* ♂ may vary considerably. Text-fig. 1*e* shows a typical *Primrose* capsule from an intraspecific cross, while Text-figs. 1*f* and *g* show large and small capsules produced in different interspecific crosses. The range in mean capsule length in nine crosses made in 1946 is shown in Table 3. A different *Primrose* parent was used in each of these crosses; there were three different *Oxlip* males.

It will be seen from the table that the longer capsules tend to have the heavier seeds, though cross 8 is a marked exception. It is also noteworthy that the largest capsules obtained, from cross 9, are of about the same size as those from the intraspecific cross, though the seed weight is markedly lower (seed weights are further described below).

Table 3. *Fruit size in Primrose ♀ × Oxlip ♂ crosses, 1946*

Cross ...	1	2	3	4	5	6	7	8	9	<i>Primrose</i> × <i>Primrose</i>
Capsule length (mm.) (no. measured in brackets)	4.6 (3)	4.9 (4)	5.2 (2)	5.3 (8)	5.7 (5)	5.7 (6)	5.9 (6)	6.0 (5)	7.9 (5)	7.8 (4)
Mean seed weight (mg.)	0.25	0.25	0.3	0.3	0.3	0.35	0.35	0.2	0.55	1.3

The size of capsules produced in the cross *Oxlip* ♀ × *Primrose* ♂ is less variable than in the reciprocal cross, as shown by the figures for capsule length in Table 4.

Table 4. *Fruit size in Oxlip ♀ × Primrose ♂ crosses, 1946*

Cross ...	1	2	3	4	5	<i>Oxlip</i> × <i>Oxlip</i>
Capsule length (mm.) (no. measured in brackets)	12.7 (5)	13.2 (5)	14.9 (5)	15.2 (10)	15.5 (3)	13.9 (4)
Mean seed weight (mg.)	0.4	0.45	0.3	0.9	0.75	1.15

It is noteworthy here that the capsules from these interspecific crosses are of roughly the same length as those from the intraspecific crosses (Text-figs. 1*a*, *b*), and this conclusion is borne out by an examination of the capsules from the 1937-40 experiments, figures for which are not presented here. It can thus be concluded that, in interspecific crosses, capsule development is more or less normal when *Oxlip* is female parent, but generally subnormal when *Primrose* is female parent. A similar conclusion was reached by de Vries (1919).

(b) *Character of seeds set*

Weights and brief descriptions of the seeds set in the inter- and intraspecific crosses are given in Table 5. Where *Primrose* was female parent, the presence or absence in noticeable quantity of the gummy substance on the placenta, described above, is noted. In each cross listed here several flowers were pollinated, and the seeds from the individual

capsules lumped in order to obtain the mean seed weight. For comparison with Table 5 some of de Vries's data are given in Table 6; they are divided into two series, A and B.

Table 5. *Description of seeds from Primrose and Oxlip crosses*

Type of cross	Year	Mean seed wt. in mg. from each cross in order of magnitude	Stickiness	Description of seeds
Primrose ♀ × Oxlip ♂	1937-40	0.5, 0.4, 0.3, 0.3, 0.3, 0.2, 0.2, 0.2, 0.2, 0.2, 0.1, 0.1	Noted in 2 crosses out of 12	Generally small and uniform, rarely 1 or 2 larger seeds (up to 0.6 mg.) in a capsule
Primrose ♀ × Oxlip ♂	1946	0.55, 0.35, 0.35, 0.35, 0.3, 0.3, 0.3, 0.25, 0.25, 0.2	Noted in 2 crosses out of 10	Generally small and uniform, rarely 1 or 2 larger seeds in a capsule
Primrose × Primrose	1938, 1946	1.3, 1.3	Seeds very sticky in both crosses	Large, uniform
Oxlip ♀ × Primrose ♂	1937-9	0.1, 0.2, 0.2, 0.5, 0.55, 0.55	—	Either small or else varying in size from small to rather large. In one cross not re- corded in col. 3, the 20 heaviest seeds averaged 1 mg.
Oxlip ♀ × Primrose ♂	1946	0.3, 0.4, 0.45, 0.75, 0.9	—	Variable in size from small to large
Oxlip × Oxlip	1938-9, 1946	0.9, 1.0, 1.0, 1.15, 1.25	—	Rather large, uniform

Table 6. *de Vries's data on seeds from Primrose-Oxlip crosses*

Type of cross	Mean seed wt. in mg.	
	Series A	Series B
Primrose ♀ × Oxlip ♂	0.15	0.25
Primrose × Primrose	0.75	0.9
Oxlip ♀ × Primrose ♂	0.7	0.4
Oxlip × Oxlip	0.9	0.85

The main fact emerging from the results in Table 5 is clear; in the intraspecific crosses, large heavy seeds are produced; in the interspecific crosses, smaller and lighter seeds. Further, in both the interspecific crosses there is considerable variation in mean weight from cross to cross, the extremes recorded being 0.1 and 0.55 mg. when Primrose is the female parent and 0.1-0.9 mg. when Oxlip is the female parent.

With the main point of the conclusions de Vries's data (Table 6) are in good agreement. Thus from Table 5 the averages of the mean seed weights for the Primrose ♀ × Oxlip ♂ crosses in 1937-40 and 1946 respectively are 0.25 and 0.3 mg.; these compare with de Vries's figures of 0.15 and 0.25 mg. Similarly for the Oxlip ♀ × Primrose ♂ cross, our average figures are 0.35 and 0.55 mg. against de Vries's figures of 0.4 and 0.7 mg. It will be noted that such differences as there are between the two sets of data are consistent, viz. our data indicate heavier seeds in the intraspecific crosses and in the Primrose ♀ × Oxlip ♂ crosses and lighter seeds in the Oxlip ♀ × Primrose ♂ crosses.

Our results and those of de Vries are also in agreement as regards the variation in mean seed weight from cross to cross in the interspecific crosses. Thus de Vries, using a single

clone of Oxlip as female parent, crossed it with three different Oxlip male parents and also with eight different Primrose male parents. With the Oxlip \times Oxlip crosses, she obtained mean seed weights of 0.85, 0.9 and 0.95 mg., with the Oxlip \times Primrose crosses, seed weights of 0.25, 0.3, 0.5, 0.55, 0.6, 0.65, 0.9 and 1.05 mg. The number of seeds per capsule did not vary significantly.

It is a reasonable deduction from these results that there are genetical factors present in Primrose and Oxlip which affect the weight of the seeds produced from a cross between any two particular individuals. This can be conclusively proved by repeating, in successive years, identical crosses between pairs of the same individuals; any differences in the seed weight from the crosses should then be maintained. We have, as yet, only two cases in which this has been done. A particular Oxlip $\varnothing \times$ Primrose σ cross gave, in 1938, seeds with a mean weight of 0.1 mg., and in 1939 of 0.2 mg.* A particular Primrose $\varnothing \times$ Oxlip σ cross gave, in 1939, seeds with a mean weight of 0.3 mg., and in 1940 of 0.4 mg. The results are thus hardly adequate as yet to confirm the conclusion we have drawn.

Yet another point emerges from the notes in Table 5, viz. that in any particular cross the small seeds from Primrose $\varnothing \times$ Oxlip σ are fairly uniform in size, while in the reverse cross they are on the whole larger and very variable in size. This variability, which extends to weight as well as size, is shown by data obtained both in our experiments and those of de Vries, some of which are given in Table 7.

Table 7. Variation in seed weight, Oxlip $\varnothing \times$ Primrose σ . Four different crosses

Cross	No. of seeds produced	Mean wt. (mg.)	
		20 heaviest seeds	Remainder of seeds
1	249	0.9	0.5
2	193	0.9	0.5
de Vries: 3	48	1.4 (8 good seeds)	0.4
4	33	0.6 (24 good seeds)	0.15

In all these cases there is a more or less continuous range of variation from large to small seeds and from heavy to light, but size is not necessarily a criterion of weight, as many of the large seeds are empty and light. Indeed, a further analysis of the seeds by dissection is necessary to explain the phenomenon.

(c) Dissection of seeds

It is fairly easy to dissect the seeds, though the small size of some introduces difficulties. The seeds are soaked in water for several days, and are then squashed under a small flat scalpel. The embryo can, with care, be squeezed out intact, though sometimes further dissection with needles under a lens is necessary to obtain it. Sections through the seeds were also cut.

Although de Vries does not report any systematic dissection, she mentions the fact that seeds from the cross Oxlip $\varnothing \times$ Primrose σ may lack either embryo or endosperm or both. This we have confirmed.

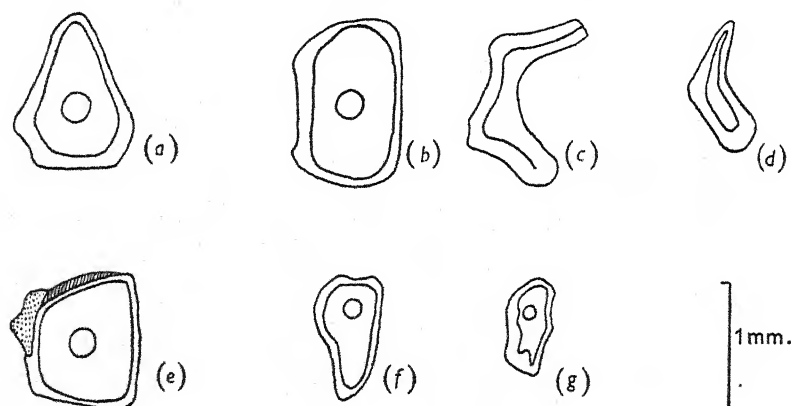
Sections through typical seeds are shown in Text-fig. 2. Comparatively little variation was found in seeds from intraspecific Primrose or Oxlip crosses, or in seeds of either

* The cross gave exceptionally poor seeds.

species collected from wild habitats. In both cases the seeds were usually plump, and contained a fairly large embryo surrounded by a mass of endosperm (Text-figs. 2*a*, *e*). On the other hand, seeds from the cross Oxlip ♀ × Primrose ♂ showed great variability not only in size but in contents. Some were very similar to Oxlip × Oxlip seeds (Text-fig. 2*b*), others were thinner and had a smaller amount of endosperm, and others were quite empty, the two sides of the seed coat being tightly pressed together (Text-fig. 2*c*). Seeds from the cross Primrose ♀ × Oxlip ♂ showed a reduction in amount of endosperm (Text-fig. 2*f*) as compared with Primrose seeds.

These data are amplified by the results of the dissections which are given in Table 8. The embryos, after removal from the seeds, were mounted in lactophenol-cotton blue, and their lengths were measured under the microscope using a micrometer eyepiece.

A number of striking points emerge from Table 8, which throw light on the data already presented in Tables 5-7. The seeds from intraspecific Primrose or Oxlip crosses



Text-fig. 2. Sketches showing cut surfaces of halved, soaked seeds. (a) Oxlip × Oxlip, 1939; normal, showing testa, endosperm and embryo. (b) Oxlip ♀ × Primrose ♂, 1937; seed with well-developed embryo and endosperm. (c) Oxlip ♀ × Primrose ♂, 1946; seed empty, but testa well developed. (d) Oxlip ♀ × Primrose ♂, 1937; seed small, lacking embryo, but with testa and endosperm. (e) Primrose × Primrose, 1938; normal, seed with well-developed embryo and endosperm; the aril (dotted) is shown. (f) and (g) Primrose ♀ × Oxlip ♂, 1946; both seeds complete, but embryo and endosperm small.

are, with few exceptions, good, containing healthy embryos of mean lengths of 80-90 units, and abundant endosperm. The seeds from the cross Primrose ♀ × Oxlip ♂ are, as was shown previously, comparatively small and light, but a high proportion (about 90% of those dissected) contain both embryo and endosperm, which are definitely though poorly developed. In sharp contrast is the very low proportion of seeds (20% of those dissected) from the cross Oxlip ♀ × Primrose ♂ which contain both embryo and endosperm; the seeds from this cross are in many cases quite large but empty.

Table 8 also shows that the average length of the developed embryo from the cross Primrose ♀ × Oxlip ♂ is 30-50 units, extremes of 25 and 81 being recorded; this is significantly less than the length of the embryo from the Primrose × Primrose cross, which is about 80 units. In the reverse cross, Oxlip ♀ × Primrose ♂, the average length of those embryos which develop is about 80 units, i.e. about the same as that from the two intraspecific crosses, though the range, 35-116, is very wide.

The seeds described in Table 8 were selected so as to be representative of nearly all the

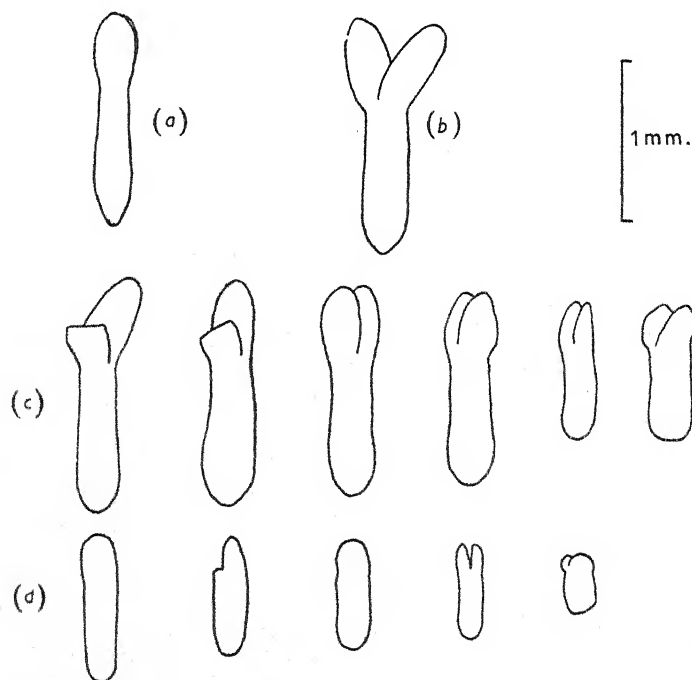
Table 8. Dissection of seeds from Primrose-Oxlip crosses

Origin of seed	Breadth of soaked seed (mm.)	No. examined	No. lacking both embryo and endosperm	No. lacking either embryo or endosperm	Lengths of embryo dissected out (arbitrary units)*
Primrose ♀ × Oxlip ♂, 1939	$\frac{1}{2}$ – $\frac{3}{4}$ mm., fairly uniform	15	1	0	41, 40, 38, 34, 31, 30, 30, 29 (mean = 30)
Primrose ♀ × Oxlip ♂, 1940	$\frac{1}{2}$ –1 mm., fairly uniform	11	0	0	63, 57, 50, 45, 40, 38, 34, 30 (mean = 45)
Primrose ♀ × Oxlip ♂, 1946 (a)	—	11	1	1 (lacked embryo)	58, 40, 30
Primrose ♀ × Oxlip ♂, 1946 (b)	$\frac{1}{2}$ mm., uniform	14	1	1 (lacked embryo)	36, 35, 34, 34, 33, 32, 28 (mean = 33)
Primrose ♀ × Oxlip ♂, 1946 (c)	$\frac{1}{2}$ –1 $\frac{1}{4}$ mm., rather variable	7	0	0	75, 70, 62, 55, 50, 50, 40, 25 (Text-fig. 3) (mean = 53)
Primrose ♀ × Oxlip ♂, 1946 (d)	$\frac{1}{2}$ –1 mm., fairly uniform	14	1	1 lacking embryo, 1 embryo and endosperm, both very small	81, 63, 57, 56, 54, 46, 40, 25 (Text-fig. 3) (mean = 53)
Primrose × Primrose, 1938	1 $\frac{1}{4}$ mm., uniform	10	0	0	90, 89, 80, 79, 75, 74, 70, 64 (Text-fig. 3) (mean = 78)
Primrose × Primrose, 1946	1–1 $\frac{1}{4}$ mm., fairly uniform	24	0	0	109, 99, 95, 90, 88, 88, 87, 85, 84, 83, 78, 78, 75, 64, 63 (mean = 84)
Oxlip ♀ × Primrose ♂, 1937	1–2 mm., variable	16	7	2 (lacked endosperm)	109, 96, 92, 82, 80, 60, 59 (35, from seed lacking endosperm) (mean = 76)
Oxlip ♀ × Primrose ♂, 1939	$\frac{1}{2}$ mm., fairly uniform	14	7	6	The 1 good embryo was broken; in 6 seeds only tiny mass of ? (embryo + endosperm) at one end of seed
Oxlip ♀ × Primrose ♂, 1946 (a)	$\frac{1}{2}$ –2 mm., variable	11	8	3 (lacked embryo)	Of the 3 seeds lacking embryo 2 had only thin shell of endosperm; in the 3rd it was well developed
Oxlip ♀ × Primrose ♂, 1946 (b)	$\frac{1}{2}$ –2 mm., very variable	23	21	0	Of the 2 seeds with contents, 1 had well-developed embryo and endosperm, in the other both were very small
Oxlip ♀ × Primrose ♂, 1946 (c)	$\frac{1}{2}$ –2 mm., very variable	25	15	1 (lacked embryo)	116, 105, 99, 92, 67, 65, 60, 50 (Text-fig. 3) (mean = 82)
Oxlip ♀ × Primrose ♂, 1946 (d)	1–2 mm., rather large variable 1 $\frac{1}{4}$ mm., fairly uniform	11 12	7 0	2 (lacked embryo)	116, 92 115, 95, 95, 94, 87, 83, 82, 82, 82, 72, 62 (mean = 87)
Oxlip × Oxlip, 1946	1–1 $\frac{1}{4}$ mm., variable	25	1	1 (lacked embryo)	116, 103, 103, 98, 98, 98, 97, 97, 93, 93, 92, 90, 80, 88, 87, 50, 39 (mean = 90)

* 69 units = 1 mm.

seeds that have been obtained, and there is no doubt that the results are typical.* It thus appears that when the interspecific cross is made with Primrose as female parent, rather poor embryos in rather poor endosperm are uniformly obtained; when the cross is made the other way, with Oxlip as female parent nothing at all is obtained in four-fifths of the seeds, but the remaining one-fifth has well-developed embryos and fairly, sometimes very well-developed endosperm. Rarely with either cross, endosperm may be developed but not embryo, or vice versa.

Outline sketches of some typical embryos which were dissected out are shown in Text-fig. 3. In some cases (not figured) the embryos, especially the smaller ones, are markedly curved, swollen or otherwise deformed.



Text-fig. 3. Sketches of embryos dissected out from soaked seeds and mounted in lactophenol-cotton blue. (a) Primrose \times Primrose, 1938. (b) Oxlip \times Oxlip, 1939; the embryo has been slightly squashed and the cotyledons spread out. (c) A series of embryos from a single cross of Oxlip $\text{f} \times$ Primrose m (1937, Table 8). (d) A series of embryos from a single cross of Primrose $\text{f} \times$ Oxlip m (1946d, Table 8).

(d) Germination

Results for the season 1946-7 are not yet available, and the data presented are therefore only for the period 1937-40.†

Seeds were sown either in Merton compost or on moist filter-paper in Petri dishes. Germination was observed, both in the autumn of the year the seeds were produced and also in the following spring. It is probable that both Primrose and Oxlip are normally

* Very small, uniform seeds were obtained in one or two particular Oxlip $\text{f} \times$ Primrose m crosses, and these have not been considered.

† For preliminary 1947 germination results, see note at end of paper.

spring germinators, but in both Oxlip and Oxlip-Primrose hybrid, a good deal of germination may take place within three or four months of seed production. In the case of Oxlip, limited germination in autumn may be followed by heavy additional germination in the following spring. The results are summarized in Table 9.

Table 9. *Germination of Oxlip-Primrose hybrid seed, 1937-40*

Type of cross	Total no. of seeds sown	No. of seedlings obtained	% germination
Primrose ♀ × Oxlip ♂	1245 (8 batches)	1	0.12
Primrose × Primrose	{ 10 (1 batch)	8 (fresh seed)	—
Oxlip ♀ × Primrose ♂	{ 159 (8 batches)	4 (seed 1 year old)	5
		38 (some germination in 4 batches)	
Oxlip × Oxlip	349 (4 batches)	76 (some germination in 2 batches)	22

The data for the intraspecific crosses are rather limited, especially for Primrose, where a figure for percentage germination has not been quoted in the table. It may, however, be noted that individual small batches of Primrose and Oxlip seeds have given germinations of 80 and 50% respectively. These figures are far in excess of anything obtained for the interspecific crosses.

Table 9 shows that of all the seeds sown from Primrose ♀ × Oxlip ♂ crosses, only one seedling has been obtained. This germinated in the spring of 1940 from a batch which had a mean seed weight of 0.2 mg., but which contained six larger seeds averaging 0.5 mg. in weight. It is probable that the single seedling obtained came from one of the larger seeds, and that the embryo and endosperm of the seed were of the fairly well-developed type which occasionally arises in this cross. Unfortunately, owing to war circumstances, the seedling was not raised to maturity.

Of the eight batches of seeds from the cross Oxlip ♀ × Primrose ♂, some germination occurred in four batches; the numbers obtained in the individual batches were 1, 3, 13, 21. The mean seed weights of these batches were not recorded, but in every batch there were at least 20 larger seeds averaging 0.9-1.0 mg. in weight. These would probably be of the type containing well-developed embryos such as are described in Table 8 and Text-fig. 3c.

The results of these germination experiments can be correlated with the nature of the embryos described in Table 8. It would appear that, where the embryo is undersized, and the endosperm poorly developed, as in the cross Primrose ♀ × Oxlip ♂, successful germination is a rare event. In the reverse cross, though many of the seeds formed are empty, those that are filled contain a proportion of embryos comparable in size with those from the intraspecific cross, and it seems likely that such seeds, provided that endosperm is fairly well developed, can germinate and survive. If it be supposed that a hybrid embryo must exceed 90 units in length to be capable of successful germination, Table 8 shows that in the Primrose ♀ × Oxlip ♂ cross no embryo out of the 72 seeds examined reaches this length, while in the 100 seeds from the reverse cross 9 exceed it. There is a very rough correspondence between these figures, and the percentage germinations, 0.1 and 5 respectively, which were obtained.

de Vries (1919) did many experiments on the germination of the seeds from her crosses, but unfortunately the results were reserved for another paper which was never published

(personal communication from Prof. A. Ernst). In the 1919 paper, de Vries makes it fairly clear that some germination was obtained from crosses in which Primrose was female parent, but no figures are given. A few figures are given for results from the reverse cross, but these figures deal only with seeds from crosses which were particularly successful, i.e. crosses in which the proportion of empty seeds was lower than usual and the proportion of large, full seeds high. In two such crosses, taken together, 60 seeds gave 22 hybrid plants, a germination of over 30%; this figure is, of course, not directly comparable with our figure of 5%, which includes all the seeds from several crosses, in many of which a high proportion of empty seeds occurred, but it can be said that making allowances for the differences, the two figures are probably not inconsistent.

(e) *Character of the hybrids*

Germination in both Oxlip and Primrose is epigeal and the seed coat is sometimes carried above ground with one of the cotyledons. The ovate, entire cotyledons are soon followed by the first leaf, which is cordate and slightly serrate. Most of the hybrid germinations which were observed were normal, but two of the seedlings of one family from an Oxlip ♀ × Primrose ♂ cross were weak and soon died; in one of these the radicle was abnormally short and poorly developed, in the other the cotyledons were much narrower and shorter than usual. The single seedling obtained from the cross Primrose ♀ × Oxlip ♂ was normal.

Most of the seedlings that were pricked out grew rapidly and well, and some came into flower within less than a year of their production, flowering abnormally late in July and August. Full and normal flowering then took place again in the following spring.

For various reasons not all the seedlings which germinated and were healthy were grown to maturity, but 26 out of the 36 healthy seedlings were grown to the flowering stage, the numbers so grown in the four families which showed germination being 12, 11, 2 and 1 respectively. The plants from two of the families were large and as vigorous or more vigorous than the parents; in the other two families, dwarf plants were obtained, 3 out of 11 in one case, and 1 out of 2 in the other. The family of 11 is shown in Pl. 5 A. All the members of the family are from 18 to 20 months old. Some difference in vigour may be attributable to delay in germination and random differences in environment, but there can be no doubt that the three dwarfs were genetically distinct from the larger plants; within the latter there was probably also some differences in size and vigour.

The large and vigorous hybrid plants are very similar to those which are usually identified as Oxlip-Primrose hybrids in the field. The latter have been described more than once, most recently by Melville (1936). A brief description of the large artificial hybrid is given here; it may be compared with the description of the parents given above; a single plant is shown in Pl. 5 B.

Characters of the Oxlip-Primrose hybrid

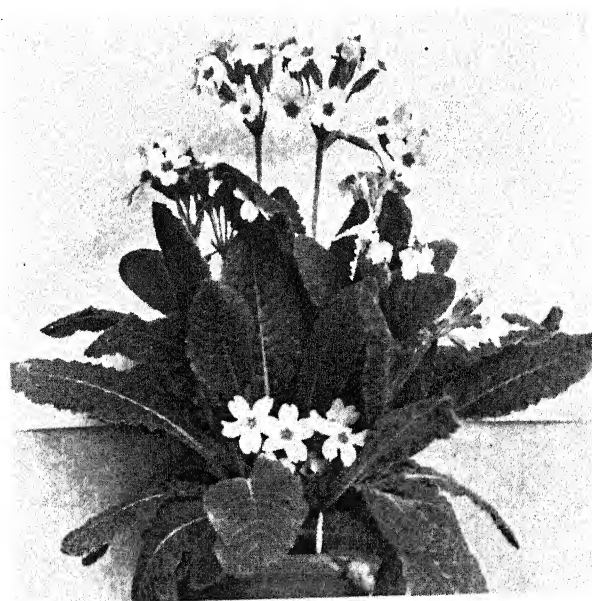
Leaves. Intermediate in shape between those of the parents; often show contraction to the petiole typical of the Oxlip.

Inflorescence. Generally pedunculate, as in Oxlip, but often, especially when flowering begins, producing single flowers like the primrose. Flowers tend to spread radially in the umbel and not to droop to one side, as in the Oxlip.

Calyx. Intermediate in shape between those of the parents, teeth shorter than in



A. Family of 11 hybrids from a cross of Oxlip ♀ × Primrose ♂.



B. A single large hybrid from a cross of Oxlip ♀ × Primrose ♂.

Primrose, longer than in Oxlip. Length of calyx and of teeth a variable character both in parents and in hybrid.

Corolla. Rather Primrose-like but limb not so broad, petals generally not so broad or so long; like Primrose has folds and a pentagonal eye-spot at the mouth of the corolla, but eye-spot is coloured orange like the ring at the throat of the Oxlip corolla.

Capsule. Erect, exceeding calyx, as in Oxlip. Placenta dry as in Oxlip, not secreting gummy substance as in Primrose.

Hairiness. Resembling Primrose in having shaggy indumentum on pedicels, though this is generally less dense than in Primrose.

The dwarf plants remained small during the whole period which they were observed. They were carefully cultivated in a good compost, but the leaves retained a chlorotic appearance, in contrast to the full, dark green of the large sister plants; in one plant the leaves were constantly deformed, being markedly convex above and concave below. Two of the plants produced inflorescences, which resembled in miniature those of the large plants; the number of flowers produced was small, and in the flowers themselves the calyx was only half the length of the corolla tube (in the large hybrids it was usually two-thirds of the corolla tube or equalled it). In colour characters, the flowers were of the hybrid type described.

This variation in size of hybrids is perhaps to be correlated with the variation in size of the embryos that has been described. Thus in the cross Oxlip ♀ × Primrose ♂, 1937, which is listed in Table 8, it is seen that the lengths of the embryos from those seeds which contained endosperm are 100, 96, 92, 82, 80, 60 and 59 units; if it be supposed that on germination the two smallest embryos give dwarf plants and the rest large plants, we should have two dwarfs to five large, a ratio very roughly approximating to the three dwarfs to eight large which was observed in the family of hybrids shown in Pl. 5 A.

(f) *Fertility of the hybrids*

The data which have been presented enable the fertility of the Primrose-Oxlip cross to be assessed. In order to interpret the phenomena seen in field populations, it is important to know something about the fertility of the hybrids themselves. Heslop Harrison (1931) has reported the raising of an F_2 generation from the Primrose-Oxlip hybrid, and also successful crosses between the hybrid and both parents, but he does not give details of the experiments. Melville (1936) has also stated that he has shown by experiment that the hybrid is fertile. The crosses we have made confirm the fact of fertility and add some details of interest.

It was hoped when the crosses were made to raise large families of the offspring, in order to aid in identifying the hybrid forms met with in the field. Because of the war, the second generation hybrids could not be carried beyond the seedling stage, and the plants obtained will not, therefore, be described here. Work towards producing another second generation is in progress.

The results obtained are given in a condensed form in Table 10.

In these crosses 8 different hybrid plants were used, 6 from one family and 2 from another, 5 Primroses and 5 Oxlips. In every backcross except one, the Primrose and Oxlip plants used were not identical with either parent plants of the hybrid. Only two crosses were made which did not give at least moderately large seeds, and these are noted

in the table. It is of interest that the same two plants were used in each of these crosses, which were reciprocals. No other exact reciprocals were made.

Table 10. F_2 and backcrosses from the Oxlip-Primrose hybrids, 1938-9

Type of cross	No. of crosses	No. of pollinations	No. of fruits obtained	Character of seeds	Mean seed wt. (mg.) (no. of seeds weighed in brackets)	Germination
Oxlip ♀ × Hybrid ♂	3	11	11	Uniform, rather large	1.0 (285)	24/156 15%
Hybrid ♀ × Oxlip ♂	3	23	18	Varying from very small to large	0.8 (420)	27/335 8%
Primrose ♀ × Hybrid ♂	3	14	12	In 2 crosses rather small and uniform (3rd cross, seeds very small, not weighed)	0.6 (250)	27/234 12% (3rd cross excluded)
Hybrid ♀ × Primrose ♂	3	29	29	In 2 crosses uniform, rather large (3rd cross, seeds small, 0.25 mg.)	1.2 (695)	67/236 28% (3rd cross excluded)
Hybrid × Hybrid	4	21	21	Some very variable, some uniform, rather large	1.0 (345)	64/335 19%

The results in Table 10 may be compared with those for the F_1 Primrose-Oxlip cross, which are given in Tables 5 and 9. For Primrose ♀ × Oxlip ♂, mean seed weight was 0.3 mg. and germination 0.1%, for Oxlip ♀ × Primrose ♂ mean weight of seed was 0.45 mg. and percentage germination 5%. Although the data for the F_2 and backcrosses are not so extensive as those for F_1 , the conclusion is clear that on the whole, the seeds are both heavier and have higher percentage germination than the F_1 .

One of the crosses included in Table 10 is that of a dwarf hybrid by a large hybrid. The dwarf hybrid, which was the female parent, set seed, some of which germinated. Thus the dwarfness of the plant did not, in this case, adversely affect its fertility.

Some seeds from each of the different types of cross listed in Table 10 were dissected; the results obtained are shown in Table 11.

Table 11. Dissection of seeds from F_2 and backcrosses

Type of cross	No. of seeds examined	No. of seeds with both embryo and endosperm	Length of embryos dissected out (arbitrary units)*
Oxlip ♀ × Hybrid ♂	10	10	95, 82, 82, 82, 80, 69, 67, 61 (one very small, broken)
Hybrid ♀ × Oxlip ♂	31	30	95, 91, 88, 86, 83, 79, 76, 75, 69, 61, 58, 44, 20
Primrose ♀ × Hybrid ♂	10	9	106, 97, 89, 88, 72, 66, 63
Hybrid ♀ × Primrose ♂	19	16	96, 93, 93, 92, 91, 88, 88, 80, 80, 78, 48
Hybrid × Hybrid	13	13	98, 96, 86, 83, 80, 76, 76, 70, 62, 48

* 69 units = 1 mm.

These results show, first, that complete failure, i.e. the production of seeds lacking in both embryo and endosperm, which is such a marked feature of the cross Oxlip ♀ ×

Primrose ♂ (Table 8) does not occur in any of the second generation seeds. The highest proportion of empty seeds in any one cross noted in Table 11 is 3 out of 19, and care was taken to see that the seeds examined and described in Table 11 were fairly representative of all the seeds of the cross. Secondly, the size of embryo produced in the second generation crosses is, on the whole, comparatively large; many are of about the size of the embryos produced in intraspecific crosses. If we apply the rough assumption made above, that an embryo must exceed 90 units in length in order to be able to germinate successfully, then we should expect to obtain some germination in all the above crosses, which is actually the case, and we should also expect the cross Hybrid ♀ × Primrose ♂ to show the highest percentage germination. This expectation is also confirmed by the results of Table 10.

On the whole then, F_2 and backcross seeds differ from F_1 in showing fewer complete failures, larger embryos and higher percentage germination.

V. DISCUSSION OF RESULTS

In general, the data we have presented are not at variance with those of other workers, in particular de Vries (1919). Heslop Harrison (1931), however, differs on an important point. He reports the success of Primrose-Oxlip crosses, and does not comment on any difference in seed production or germination between the reciprocal crosses, both of which were made. He mentions specifically a cross of *P. vulgaris* var. *purpurea* Maul. ♀ by *P. elatior* ♂, the seed from which 'germinated freely to yield a large number of hybrid plants'; among these hybrids were four dwarf plants which did not flower, but which resembled Oxlip in leaf characters. They proved, on cytological examination, to be, in part, haploid, many cells having only 11 chromosomes instead of the normal number of 22.

In his experiments, which dealt with many species of the section *Vernales* other than Primrose and Oxlip, Harrison used stocks from a wide range of localities, both British and Continental; and it would appear that he hit upon certain stocks of Primrose and Oxlip which, when crossed, gave a high yield of fertile seed even though Primrose was the female parent. Both we and de Vries have observed that the weight and character of seed produced may vary considerably from cross to cross; in our experiments, as has been shown, the yield of germinable seed has so far been very small, and one can gather from de Vries's paper only that in certain crosses, *some* germinable seed was produced when Primrose was the female parent of the cross.

In this discussion, we shall regard Harrison's result as exceptional and our own as typical. It may be mentioned that the dwarf plants obtained in our crosses (p. 240) were, as judged by foliar and floral characters, undoubtedly hybrids and almost certainly diploid.

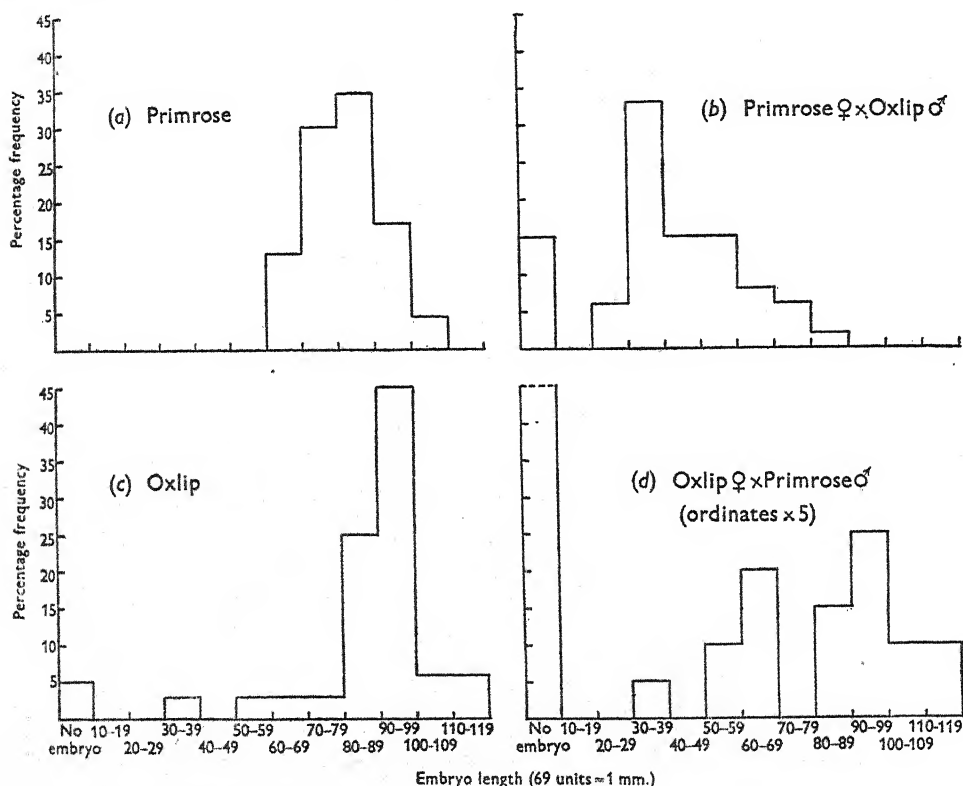
(a) Offspring of the cross Primrose ♀ × Oxlip ♂

We have seen that in this cross seeds are invariably formed, and that the seeds are smaller and lighter than those from the cross Primrose × Primrose. The data presented on embryo lengths in Table 8 are shown graphically for convenience in Text-fig. 4.

The course of pollination and fertilization in this cross has not been followed in detail, but it is clear that in 85% of the seeds these processes must occur, as embryo and endosperm are regularly formed. About 15% of the seeds are superficially sound, in that they do not differ in size from full seeds, and have a normal testa, but they are found on

dissection to be empty. The reason for this phenomenon will be discussed more fully when the seeds from the reverse cross are described; it seems likely, however, that pollination and fertilization of all the ovules does occur, but that in 15% of the seeds, irregularities occur following fertilization which lead to the early degeneration of embryo and endosperm.

Seed size is difficult to measure accurately, and we shall therefore use embryo length as the basis of discussion. Text-fig. 4 shows clearly the differences between the embryos



Text-fig. 4. The figures for embryo length given in Table 8 are here plotted as frequency diagrams. The number of embryos measured in each case was (a) Primrose, 23, (b) Primrose ♀ x Oxlip ♂, 48, (c) Oxlip, 32 and (d) Oxlip ♀ x Primrose ♂, 97. In class (d), 78% of the seeds examined lacked an embryo; in the graph for this class the values plotted as ordinates have been multiplied by 5 in order to show clearly the size distribution in the 19 embryos which were measured; and the entry in the class 'no embryo' has been curtailed, as it would extend to a value of 390. The values for the ordinates in graphs (a), (b) and (c) are correctly to scale.

from the inter- and intraspecific crosses. Reference to Text-fig. 3 makes it clear that the embryo from the Oxlip-Primrose crosses *can* develop, under appropriate conditions, to a size comparable with that from the intraspecific crosses. It would therefore appear that the small embryos characteristic of the cross Primrose ♀ x Oxlip ♂ are due to some special environmental factor. At least two such factors can be distinguished.

First there is a possible maternal effect. It has been shown (Table 3 and Text-fig. 1) that when Primrose is female parent, the ripe capsule is, in many cases, only about half the normal size, and that the size of seeds produced is roughly correlated with the size of

the capsule containing them. This suggests that pollination by Oxlip pollen may cause the Primrose capsule to ripen prematurely, and hence the seeds also to ripen prematurely; this is supported by the fact that only rarely is the gummy substance characteristic of the ripe placenta and seeds fully developed in the capsules from Oxlip pollination. It is known (Gustafson, 1942) that the stimulus of pollination is a factor which is important in causing development of the ovary, and it may be that in this case the stimulus of the Oxlip pollen is insufficient to produce normal development with consequent premature ripening.

That this hypothesis is insufficient to explain the facts is, however, shown by two further considerations. First, in certain cases (Table 3), the Primrose ovary may develop to its normal size, yet the hybrid seeds which it contains are still much smaller and lighter than in the intraspecific cross; secondly, it is probable (Gustafson, 1942) that in some cases developing ovules and seeds themselves contribute, possibly by the production of growth hormones, to the full development of capsules, i.e. that there is an effect of the seeds on the capsule, as well as an effect of the capsule on the seeds. It is thus likely that there is something in the constitution of the seeds themselves which stops their development at an earlier stage than in the intraspecific cross; and this factor may well be the endosperm.

It is likely that the health and vigour of embryo and endosperm are closely correlated. Brink & Cooper (1940) consider that the endosperm plays a vital part in the transmission of nutrients to the developing embryo, and several cases are known (one will be quoted below) in which seed abortion can be attributed to early failure of the endosperm. If the haploid chromosome sets of Primrose and Oxlip be represented by *P* and *O* respectively, it is to be presumed that the endosperm in the cross with Primrose as female parent will have the constitution *PPO*, and in the reverse cross, *POO*. It is reasonable to suppose that the hybrid embryo (of the constitution *PO* in either cross) may not thrive so well in a *PPO* endosperm as it does, in certain cases, in a *POO* endosperm.

Besides the difference in size between Primrose and hybrid embryos, Text-fig. 4 also shows a rather wider range of variation in the size of the hybrids. Embryo size is a character which is probably controlled by polygenes (Mather, 1943), and Primrose and Oxlip are both normally outbreeding species, so that individuals will probably be heterozygous for many genes. We should therefore expect that in the interspecific cross the range of variation in the size of offspring would be wider than in the intraspecific cross, due to lack of relational balance between Oxlip and Primrose genomes. In considering embryo sizes, and particularly in this case, it should be pointed out that lack of balance in the endosperm may play as important a part as lack of balance in the embryo. If the wider range of variation in the hybrids be described as the result of heterosis (Mather, 1943), then we may speak of endosperm heterosis as well as of embryo heterosis, although it is impossible in this case to disentangle the two effects.

We have already suggested that the poor germination of the seeds from this cross is due to the small size of the embryo (and possibly the small amount of endosperm too), and that embryos below a certain size do not germinate. Much additional work will be necessary before this can be confirmed; it may be found possible, by using dissection and a special culture technique (McLean, 1946), to produce artificial germination by growing the embryos on a suitable medium, although it is difficult to remove the embryos, particularly from fresh seeds, without damaging them slightly.

A fairly wide variation in size, weight and contents of seed between individual crosses has been noted above (p. 234). As different Oxlip and Primrose parents were used in the different crosses, this variation is comprehensible; for in an outcrossing population of either parent, we should expect a fair amount of genetical heterogeneity, so that variation in the parents will be reflected in variation in the hybrid seed, some combinations being more successful than others.

(b) *Offspring of the cross Oxlip ♀ × Primrose ♂*

The seeds produced in this cross are described in Table 8, and the embryos dissected from the seeds in Text-fig. 3. As has been shown, about 80% of the seeds are empty and contain neither embryo nor endosperm.

Pollination and fertilization in this cross have not yet been investigated, and the question as to whether pollination of all the ovules takes place must be raised. The evidence is in favour of the occurrence of pollination. de Vries (1919) has pointed out that when plants of Oxlip are selfed, the number of seeds produced is much below normal, and that the capsules contain *either* undeveloped ovules *or* developed seeds; it is well known that in heterostylic flowers such as those of the Oxlip, self-incompatibility is caused by the impeded growth of pollen on its own stigma and style, and it is clear that in such cases only those ovules develop which are pollinated. In 'legitimate' interspecific crosses, however, the number of seeds produced is approximately the same as in intra-specific crosses; de Vries quotes data to illustrate this, and the fact is confirmed by data of our own, which may be briefly summarized in Table 12. We may therefore conclude that in all probability a normal proportion of Oxlip ovules are pollinated by Primrose pollen tubes. The question of fertilization then arises.

Table 12. *Number of seeds in Primrose-Oxlip legitimate crosses*

Type of cross	No. of capsules investigated	Mean no. of seeds/capsule
Primrose × Primrose	8	36
Primrose ♀ × Oxlip ♂	63	43
Oxlip × Oxlip	10	33
Oxlip ♀ × Primrose ♂	46	37

We have seen that about 20% of the ovules in a capsule produce seed which contains both embryo and endosperm, so that in these cases fertilization may be presumed to occur more or less normally. It is a noteworthy fact that the remaining seeds, which are mostly quite empty, vary considerably in size, some being quite small ($\frac{1}{2}$ – $\frac{3}{4}$ mm. in diam.). Further, occasional seeds contain some endosperm, with apparently no embryo, while others have an embryo, usually minute and deformed, with little or no endosperm alongside it. The testa in all the seeds is normal in appearance.

It is conceivable that development of the testa may be stimulated by pollination, without the extra stimulus of fertilization; but if this were the case for all the empty seeds, we should expect them all to be about the same size. The fact that they vary in size would seem to indicate that in some of them at least, some nuclear fusions take place, and that failure of embryo and endosperm takes place subsequently. If embryo and endosperm develop sufficiently, the extra stimulus to testa development will be given and this may well be variable according to the extent of development of embryo and endosperm.

Further, as we know from the cross Primrose ♀ × Oxlip ♂ that at least 85% of the embryos of the constitution *PO* are capable of development, we should expect that the tissue which would most often fail after fertilization would be the endosperm.

In Text-fig. 4 are plotted the lengths of embryos from the intraspecific Oxlip cross, and of the embryos obtained in the interspecific cross. Leaving out of account the empty seeds, it may be seen that there is a great similarity in the range of length, though the mean length is slightly less in the interspecific cross than in the intraspecific. It may be concluded that, provided the initial post-fertilization stages are successfully completed, the seeds from the cross Oxlip ♀ × Primrose ♂ are not greatly inferior in embryo size (and probably in amount of endosperm too, as judged by seed weight) to those of the intraspecific cross, i.e. in some cases *PO* embryos can develop nearly as well in *OOP* endosperm as *OO* embryos in *OOO* endosperm. The difference between this result and that obtained in the reciprocal cross is marked; for in the latter it was found that the hybrid embryos were both smaller and showed a wider range of variation than Primrose embryos. This difference may be attributed to the facts, first, that the normal range in Oxlip embryos is wider than in Primrose, and secondly, that many of the embryos which might be expected to arise from the cross with Oxlip as female parent do not develop to maturity; they die at an early stage because of endosperm failure, and only empty seeds are produced.

Further development of the hypothesis advanced here must wait on embryological studies, which it is hoped to carry out. The hypothesis depends on the assumption that the range of variation in endosperm of the constitution *OOP* is very wide, and that in about three-quarters of the seeds in which it is formed, it breaks down at an early stage and causes the seed to fail; in the remaining one-quarter, the balance is good enough for development to proceed to about the same extent as it does in normal seeds. As we have seen, heterosis in the embryos is not marked, possibly for the reason we have already given, viz. that many of the embryos fail to mature; our hypothesis would postulate very marked heterosis in the endosperm; this would perhaps be stretching the use of the term, though Mather (1943) defines it as including 'all examples of poor relational balance between combinations of different wild interbreeding groups'.

It is clear that a set of seeds from the cross with Oxlip as female parent could not show more than about 20% germination; the figure of 5% which is recorded indicates that a high proportion of the full seeds does germinate, and it was suggested above (p. 239) that the seeds which germinated were those which contained embryos exceeding a certain size. It was further suggested that dwarf hybrids were produced from seeds which contained rather smaller embryos; this, of course, involves the assumption that the size of plant obtained is dependent on size of embryo rather than on a difference in relative growth rates of the germinated seedlings. This is the conclusion reached by Ashby (1937) in his work on heterosis, but Ashton (1946) quotes other workers who are in disagreement. In our case, we are unable as yet to offer any critical evidence on the point and must confine ourselves to making the suggestion.

(c) The F_2 generation and the backcrosses

Before discussing the F_2 results, brief reference may be made to the cytology of the species, so far as it is known. Many counts have been made of somatic chromosome numbers in Primrose and Oxlip during the last twenty years, e.g. those of Heslop Harrison (1931) and Bruun (1932), and all have given the same result, viz. $2n = 22$, for both species.

Chittenden (1928) examined reduction divisions in the pollen mother cells of the hybrids *P. vulgaris* \times *P. juliae* and *P. elatior* \times *P. juliae*; he found that 'reduction divisions... were surprisingly regular'; he also noted 50-70% of apparently good pollen in the hybrids. We have as yet made no cytological analysis of our material; cursory examination of the pollen of the F_1 hybrids, using acetocarmine staining, has shown a proportion of good pollen at least as great as that noted by Chittenden in his hybrids. It is thus probable that meiosis in the Primrose-Oxlip hybrid is regular, and there is no reason to expect a heavy reduction in its fertility because of cytological irregularities.

That the F_1 hybrid can function efficiently both as pollen and as seed parent is shown by our results (Table 10). We may add that the number of seeds per capsule formed in these crosses is not significantly different from the typical number of 30-40 reported above. A further point of interest is that the proportion of empty seeds is very low, i.e. pollination is regularly succeeded by fertilization and successful development of a full seed. If the sizes of the embryos be examined (Table 11) it will be seen that the range is not very different from that of Oxlip seeds, though rather wider than that of Primrose seeds.

We must conclude that the factors which so greatly reduced the formation of good seed in the first generation of the cross have largely disappeared in the second generation. Now the hybrids used in making the second generation crosses were the successful hybrids from the cross Oxlip $\varnothing \times$ Primrose σ , i.e. they were hybrids with the constitution *OP* which had developed in an *OOP* endosperm, and, on our hypothesis, in a well-balanced *OOP* endosperm, since we supposed that many endosperms of this type failed to develop to any extent. Let us consider the backcrosses Hybrid $\varnothing \times$ Primrose σ and Hybrid $\varnothing \times$ Oxlip σ . If we suppose that Oxlip chromosomes pair with Primrose chromosomes and separate at random, then the constitution of the seeds most commonly found

in the cross Hybrid $\varnothing \times$ Primrose σ will be $\left(\frac{O}{2}, \frac{P}{2}, P\right)$ embryo in $2\left(\frac{O}{2}, \frac{P}{2}\right)P$ endosperm, i.e. *OPP* endosperm. This endosperm in combination with *OP* embryos gives, as we have seen, small seeds which germinate very poorly; but the *O* and *P* genomes which it contains in the second generation seeds will not be the same as in the first generation, as they will have been selected for balance from the first generation seed, and may therefore be expected to give a better result. Similarly, the constitution of the seeds from the cross Hybrid $\varnothing \times$ Oxlip σ can be written as $\left(\frac{O}{2}, \frac{P}{2}, O\right)$ embryo in *OOP* endosperm. Again,

the endosperm of this constitution, which has such bad effects in the F_1 seeds, has been improved as a result of selection of good seeds from the F_1 , though the range of variation in embryo size is greater, and the percentage germination lower (8% as against 26%) than in the cross Hybrid $\varnothing \times$ Primrose σ . In view of the paucity of the data, it is not admissible to push the analysis any further; but whatever hypothesis be adopted, it is clear that selection of viable combinations in the F_1 has led to an improvement of 'crossability' and viability of seeds in the F_2 and backcrosses.

Attempts to obtain viable hybrids from the cross Primrose $\varnothing \times$ Oxlip σ are being continued; it is conceivable that such a hybrid, the product of an *OP* embryo in a *PPO* endosperm, though perhaps identical in appearance with the reciprocal hybrid, would behave differently on selfing and backcrossing, for its genomes would have been selected for a good balance in a *PPO* endosperm, and might therefore differ from those of the reciprocal hybrid, whose genomes had been selected for balance in an *OOP* endosperm.

VI. GENERAL DISCUSSION

The disparity between the results of reciprocal crosses between Primrose and Oxlip is not by any means a unique case. Watkins (1932) has described numerous crosses between plants in a polyploid series which have different chromosome numbers, and has shown that pollinations between two species succeed more often when the parent with the higher chromosome number is the female than in the reciprocal cross; and other workers, e.g. Boyes & Thompson (1937) and Howard (1939), have produced further evidence in support of this. With respect to species having the same chromosome number, no general hypothesis has been advanced; in this connexion the work of Jenkin and his collaborators (1932, 1933, 1935, 1939) is of interest. In particular, the results of Jenkin (1933) with the species *Lolium perenne* and *Festuca pratensis*, which both have $2n=14$, provide a striking parallel to our results with Primrose and Oxlip. Jenkin's results may be briefly summarized as follows:

Lolium perenne ♀ × *Festuca pratensis* ♂

Fruits variable in size, some developing little, if at all, others to about half normal size. Fruits plump, containing well-organized endosperm but only in small amount. About 1% germination.

Festuca pratensis ♀ × *Lolium perenne* ♂

Fruits variable in size from about half normal to normal or slightly larger. Fruits mostly shrivelled, often deformed, empty or containing only a watery fluid in place of endosperm. About 5% germination.

Only those fruits were examined which failed to germinate, so that there is no information about the successful seeds.

The close resemblance to our cross, the *Lolium* corresponding to the Primrose and the *Festuca* to the Oxlip, is clear. Jenkin discusses these results fully, referring in passing to their marked similarity to those obtained by Kihara & Nishiyama (1932) in their cross of diploid *Avena strigosa* with hexaploid *A. fatua*. He comes to very much the same conclusion as we have done, viz. that the difference between the cross and its reciprocal is mainly shown in a difference in development of endosperm, which is different in constitution in the two cases; and he also emphasizes that this type of result is not necessarily correlated with a difference in chromosome number between the species concerned. Howard (1942), in analysing the seeds of crosses between a number of diploid, auto-tetraploid and allotetraploid species of *Brassica*, finds that in most cases the results follow Watkins's rule (quoted above), but suggests that some allotetraploid species may have evolved so as to have a 'diploid physiology', i.e. they will produce normal seeds when crossed in either direction with a diploid species. Our results and those of Jenkin suggest that the converse may also hold, i.e. that certain diploid species may have evolved so as to have a 'tetraploid physiology'. It is at any rate clear that a simple explanation of the failure of reciprocal crosses on the lines suggested by Watkins (1932), i.e. in terms of lack of balance in chromosome number between embryo and endosperm, cannot hold in all cases, and that qualitative as well as quantitative differences in the chromosomes of embryo and endosperm are of importance.

It would be of great interest to know if behaviour of the Primrose-Oxlip type were

widespread in hybrids between species having the same chromosome number. The matter has not as yet been systematically investigated though there are clearly a number of cases which are suggestive. Thus Marsden Jones (1930) states that he was unable to make the hybrid *Geum rivale* \times *G. urbanum* using the former as female parent, while with *G. urbanum* as female parent the cross was successful, but the size and condition of the fruits obtained is not stated. Cases which resemble in general features that of *Lolium* \times *Festuca* have been described by Jenkin (1935) for *Lolium perenne* and *L. temulentum*, and Jenkin & Thomas (1939) for *L. loliaceum* and *L. rigidum*.

Another example is provided by the work of Stephens (1944) on diploid species of *Gossypium*. Stephens summarizes his data by stating, first, that crosses between Old World species produce viable seeds, and that with certain exceptions, crosses between American species also set viable seeds, provided fertilization can be effected. In crosses between Old World and American species, however, the situation is, as a rule, different; in these fertilization is readily effected, but the majority of the seeds obtained are inviable; this seed failure is attributed to some 'post-fertilization disharmony'.

A cross which is relevant to this discussion is that between barley and rye, described by Thompson & Johnston (1945). It was found that with rye as female parent, no development of either embryo or endosperm was obtained, but with barley as female parent, both embryo and endosperm developed. Embryo development was normal at first, but the endosperm was abnormal from the start; cells never formed in it, and 6-8 days after fertilization the embryo-sacs collapsed; as a consequence of endosperm failure, further growth of the embryo ceased. Barley \times rye may be described as a wide cross, and Thompson & Johnston point out that fertilization has been observed in a number of wide crosses, such as those between *Nicotiana* and *Petunia* or *Solanum*, and suggest that the failure of many of these may well be due to what they call 'post-fertilization breakdown'.

The cases of *Gossypium* and of the barley-rye crosses resemble one another in that the crosses are either between rather distantly related species or between different genera (which, however, have the same chromosome number), that fertilization takes place, and that subsequently there is a breakdown in seed formation which in the case of the barley-rye cross, is attributable to endosperm failure. The resemblance between these crosses and those of Primrose-Oxlip and of *Lolium-Festuca* are marked, so marked that we would propose tentatively the hypothesis that in crosses between distantly related species or between different genera which have the same chromosome number, fertilization may occur, but the cross will succeed better in one direction than in the reciprocal, and seed failure will be attributable to failure of endosperm rather than of embryo.

It is important to contrast the behaviour of these wide crosses, as they may be called, with crosses between species which are generally deemed to be closely related. Good examples of such species pairs with the same chromosome number are to be found in *Melandrium album* and *M. dioicum*, and in *Silene maritima* and *S. cucubalus*. The *Melandria* have been recently investigated by Löve (1944), who finds that the species will cross together in either direction, giving a full yield of fertile seed and a fertile F_2 . Turrill (1946) has reported similarly on crosses between British material of the two species of *Silene*. These cases provide a striking contrast to the Primrose-Oxlip cross and the others like it to which we have referred.

If our hypothesis be correct, it would lead to the conclusion that the Primrose and the Oxlip are not very closely related species. It is not proposed to discuss the conclusion

fully at this point, and the matter must be postponed to the second paper of this series, in which some of the geographical and ecological factors affecting the Primrose and the Oxlip will be described. We are justified, however, in making the statement that on the grounds of their behaviour when they are crossed together Primrose and Oxlip behave as though the relation between them was not a close one, as though, in fact, they belonged to different subgenera; their morphology, on the other hand, would indicate a fairly close relationship. It is possible that the two species are old species, i.e. became separate from one another a long time ago, and that they have continued to evolve in isolation from one another. Their coming together again on a large scale may be a comparatively recent event. Mather (1943) has suggested that as species differentiate and interbreeding between them decreases, the chances of the balance between their genomes being a good one become less and less, and unbalance and heterosis in the hybrids between them become more marked; this would mean that completeness of isolation and length of time of isolation are both factors which affect the phenomena observed when two species are crossed together. The species we have been discussing are all readily recognizable as distinct in the field, and their isolation may be presumed to be reasonably complete; the difference in their behaviour when crossed would then be ascribable to their age as species. It is for this reason that we suggest that Primrose and Oxlip are 'old' species and that the *Melandria* and the *Silenes* mentioned above, comparatively 'new'. Jenkin (1933) came to a similar conclusion when he stated that 'the derivation of the *Lolium* and *Festuca* diploid types from a common prototype is supposed to have occurred at a very remote period of time'.

A word may be added on the relation of these results to the cytology of the species. Peto (1933) made cytological studies of a *Lolium-Festuca* hybrid that had been made by Jenkin, and of the *L. perenne* and *F. pratensis* parents from which it arose. He found that the hybrid regularly formed seven bivalents at meiosis and that the chiasma frequency of the hybrid was not significantly lower than in either of the parents. The high degree of infertility which the hybrid showed was due to physiological disturbances which led to degeneration of the pollen at and following tetrad formation. Studies of meiosis in the Primrose-Oxlip hybrid have yet to be made, but from the information quoted above (Chittenden, 1928) and from examination of the pollen it would seem probable that meiosis occurs in the hybrid in a regular manner, and that normal pollen is mainly produced; the production of a high proportion of viable seeds in the F_2 generation is further evidence of fertility. Thus the Primrose-Oxlip cross resembles the *Festuca-Lolium* cross not only in its mode of seed formation, but probably also in the fact that the chromosomes in the hybrid pair regularly at meiosis.

This naturally leads to speculation as to the way in which genetic isolation between the species may have been achieved. It is possible that in Primrose and Oxlip, perhaps by a series of polygenic mutations, the genomes have progressively differentiated in such a way that, when they are brought together, embryo formation takes place, but unbalance in the endosperm is so great that viable hybrids rarely come to maturity. Once the hybrids are formed, they are quite fertile, the genomes of the parent populations being sufficiently variable to provide a certain proportion of well-balanced combinations in the hybrids. The apparent success of meiosis in the hybrids would indicate that there have been no major chromosomal changes.

Lolium perenne and *Festuca pratensis* have perhaps followed a similar course, but here

sterility of the hybrid, due to physiological disturbances in the post-meiotic stages, has supervened. That this course of development is not the only possible one is perhaps indicated by the phenomena observed when the Oxlip and the Cowslip (*Primula veris* L.) are crossed. Here, the results are apparently similar to those in the Primrose-Oxlip cross, but failure is more extreme, in that the formation of viable seed from the cross in either direction is, in all probability, a very rare event. It is intended to discuss this cross in detail in another paper in this series.

SUMMARY

The results of crosses between wild stocks of Primrose and Oxlip are described, and compared with those of other workers.

When Primrose is the female parent of the cross, both fruit and seed are generally subnormal in size. About 85% of the seeds contain both embryo and endosperm, but germination is very poor.

When Oxlip is the female parent of the cross, the fruits are normal in size, but about 80% of the seeds are empty, lacking both embryo and endosperm; the remaining seeds, some of which are as large as Oxlip seeds, contain embryo and endosperm and germinate fairly well.

Hybrid plants, which are described, have been reared from the cross Oxlip ♀ × Primrose ♂. When crossed *inter se* and backcrossed they are compatible and fertile; most of the seeds produced approximate to those of the parent species in size and weight, and percentage germination is higher than in the initial crosses. Adult plants of the second generation have not yet been reared.

The difference in the seeds from the reciprocal interspecific crosses is ascribed to a difference in constitution of endosperm. When Primrose is female parent, endosperm is usually formed, but development stops before the seed has reached its full size. When Oxlip is female parent, the endosperm degenerates at a very early stage, and seeds which are practically empty are produced; in certain unions, however, a balance between Oxlip and Primrose genomes is achieved, and good seeds with well-developed endosperm are formed. The success of the second generation seeds is thus due to the fact that only well-balanced combinations of genomes survive in the F_1 hybrids, the unbalanced types having been eliminated as unsuccessful seeds.

Other interspecific hybridization which is similar to that between Primrose and Oxlip is briefly reviewed; the hypothesis is advanced that behaviour of this type is characteristic of crosses between species which are not very closely related and which have the same number of chromosomes.

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Note added in proof (May 1947)

With reference to Table 9, p. 239, preliminary figures for germination of the seeds obtained in 1946 are now to hand. Most noteworthy is the good germination (19%) of seeds from the cross Primrose ♀ × Oxlip ♂. This marked contrast with the figure obtained in 1937-40 (0.1%) is most probably to be ascribed to the use of different parent stocks, particularly Primrose stocks (see discussion of Harrison's results on p. 243). Germination in the reciprocal cross (Oxlip ♀ × Primrose ♂) is 12%, and in both the pure species, 85-90%.

FURTHER EXPERIMENTS ON PLAGIOTROPISM AND CORRELATIVE INHIBITION

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From his excellent study of correlative inhibition in *Araucaria excelsa* Massart (1924) drew the following conclusion amongst others, that in this species, in which the plagiotropism of the branches is fixed from the start, inhibition does not travel up into a branch, though in a plant of the same species with more than one orthotropic leading shoot it can travel from one such shoot up another, just as also it can in seedlings of the common Leguminosae, in which all shoots are orthotropic. His evidence for this conclusion was that when the tip of a branch is cut off lateral buds grow out from the branch a little below the cut and replace the missing tip. These replacement buds are quite distinct from those which grow out normally to form the visibly different branches of the second order, and clearly they can be inhibited, since they were inhibited previously by the tip of the branch. But since they grow out when the tip of the branch is cut off, they are not inhibited by the tip of the main shoot together with the tips of the other branches, or only very little. Nevertheless the tip of the main shoot or of another branch can inhibit these replacement buds if it is grafted on to the end of the decapitated branch. So apparently in this species inhibition can travel down a branch but not up into it. (The mere fact that the branches grow does not show that inhibition cannot travel up them; for so also do two orthotropic shoots if they happen to be equally strong.)

In *Impatiens roylei* the epinastism of the branches, on which their plagiotropism depends, is induced by the tip of the main shoot; and the writer showed recently (1945) that in that species the growth of a branch is normally not inhibited at all by the main shoot and the other branches, but that if a branch is deprived of its developing leaves, then it becomes more nearly orthotropic and is also gradually inhibited. So in that species induction of epinastism and correlative inhibition are clearly alternatives which tend to exclude each other, and it therefore seemed desirable to find out whether the fact that plagiotropic branches are not inhibited is due to an inability of inhibition to travel up into them, as in *Araucaria excelsa*.

Accordingly the following experiment was performed. Seedlings of *Impatiens roylei* were grown in the open ground in half-shade until the branches of the strongest whorl near the base of each plant, three or four in number, were beginning to elongate their second internodes. Then the buds formed by each of these branches in the axils of its lowest whorl of leaves, several cm. from its base, were selected for measurement, being only 2 or 3 mm. long and from six to nine in number on each plant. Nine well-matched plants were now chosen and were divided into three groups of three. Those of group (a) were left intact, those of group (b) had the tips of the branches which carried the measured buds cut off just beyond them, and those of group (c) had the tips of those branches cut off, and also the tips of all other branches and of the main shoot, so that they were left with mature leaves only. The mean length, in mm., of the measured buds in each plant of the three groups after 17 days of cool weather in June are given in the table. Their

growth in each of the plants, except in those of group (a) was fairly uniform as the extremes show, so that it seems unnecessary to calculate probable errors.

Table. *Impatiens roylei*. Mean lengths in mm. of measured buds in each plant after 17 days

Group (a) Plant (1)	13.4	Extremes 27 and 7	Mean of 6 buds
(2)	12.3	Extremes 19 and 7	Mean of 9 buds
(3)	4.7	Extremes 7 and 3	Mean of 9 buds
Group (b) Plant (4)	30.8	Extremes 38 and 20	Mean of 6 buds
(5)	22.8	Extremes 25 and 17	Mean of 8 buds
(6)	18.9	Extremes 25 and 15	Mean of 7 buds
Group (c) Plant (7)	34.9	Extremes 43 and 30	Mean of 6 buds
(8)	26.9	Extremes 33 and 22	Mean of 6 buds
(9)	25.5	Extremes 35 and 20	Mean of 9 buds

As the table shows, the buds in groups (b) and (c) grew out practically equally, but in the intact plants of group (a) they grew much less, though they did grow a little. Since, therefore, in group (b) removal of the tips of the branches carrying the measured buds made these buds grow out much faster than those of the intact plants of group (a), the buds must previously have been inhibited by the tips of the branches carrying them. But further, since these buds grew out rapidly in group (b) and were scarcely made to grow any more rapidly in group (c), by removing in addition the tips of the main shoot and of all the numerous other branches, they cannot have been inhibited appreciably by the tips of the main shoot and of all the other branches together. So it seems to follow that in this species also inhibition can travel down a plagiotropic branch, but not upwards into it, or scarcely at all.

Massart's experiment of grafting the tip of a main shoot on to the end of a decapitated branch was not attempted, since with *Impatiens roylei* it is not needed. For this species does not form vegetative buds of permanently different kinds, as does *Araucaria excelsa*, and consequently the experiment reported is enough to show that any growing bud at the end of a branch inhibits strongly the axillary buds formed by that branch, whereas all the similar growing buds elsewhere together scarcely inhibit them at all.

A similar experiment was performed on nine seedlings of *Salvia coccinea* growing in pots in a greenhouse, another species in which the epinastism of the branches is induced by the main shoot. On the strongest pair of opposite branches near the base of each plant the two small buds formed by those branches in the axils of their second pair of leaves, several cm. from their bases, were chosen for measurement. Of these two buds, one is on the outer face of the obliquely ascending branch and one on the inner face, and the outer bud always grows the more strongly, so that outer buds must be compared with outer buds, and inner with inner. The period of the experiment was 10 days for the first of the three plants of each group, and 7 days in warmer weather for the others. After these times the lengths in mm. of the outer and inner buds in the plants of the three groups, which are given the same letters as before, were the following:

Outer buds group (a)	6.5, 7, 6, 7, 7, 5	Mean	6.4 ± 0.26
(b)	12, 14, 14, 11, 14, 19	Mean	14.0 ± 0.69
(c)	14, 15, 17, 14, 14, 14	Mean	14.6 ± 0.39.
Inner buds group (a)	2.5, 4, 4, 2.5, 3, 2.5	Mean	3.1 ± 0.19
(b)	8, 7, 4, 5, 4, 8	Mean	6.0 ± 0.47
(c)	7, 8, 9, 8, 7, 9	Mean	8.0 ± 0.22.

Thus in *Salvia coccinea* also comparison of groups (a) and (b) shows that the tip of a branch inhibits strongly the axillary buds formed by that branch, whereas comparison of groups (b) and (c) shows that the tips of the main shoot and of all the other branches together scarcely inhibit them at all. Again, therefore, it seems to follow that inhibition can scarcely travel up into a plagiotropic branch.

These results make it necessary to modify a tentative conclusion reached previously (1945). For the previous experiment of depriving a branch of *Impatiens roylei* of its developing leaves showed clearly that the inhibition of a branch and the induction in it of epinastism are alternatives; and it was concluded that this tended to support the opinion of Münch (1938) that they are equivalent, which the writer interpreted as meaning that they are different reactions to the same transmitted influence. But the present results have shown that inhibition cannot travel up a plagiotropic branch, or scarcely at all, whereas the influence inducing epinastism, which in *Impatiens* and *Salvia* is labile, clearly does travel up it. It therefore now seems more probable that these are two different transmitted influences after all, as is indeed quite possible if inhibition and induction of plagiotropism are indirect processes, in spite of the fact that the first stage in each is the same, being the secretion of auxin by the tip of the main shoot. So, apparently, the situation is that when the branches possess their developing leaves and so have abundant auxin, inhibition cannot travel up into them and the influence inducing epinastism does do so, whereas when they are without these leaves inhibition does travel up them and the influence inducing epinastism either cannot travel up into them or is not effective when it gets there.

In the previous paper (1945, p. 112) another experiment was reported in which a branch of *Impatiens roylei* was decapitated and so deprived of its developing leaves and was then given a cap of lanoline containing hetero-auxin at 1 in 350. The result was that it remained dorso-convex like an intact branch, whereas a similar branch similarly treated but without hetero-auxin curved, as usual, dorso-concave. But since this was done on one pair of branches only, the experiment has now been repeated as follows.

In each of three seedlings of *Impatiens roylei* two similar branches of a lower whorl, a few cm. long, had their tips cut off, and one of them was capped with lanoline containing hetero-auxin at 1 in 350 and the other with vaseline. In 8 days of cool weather the branches curved so that the inclinations of their ends were changed by the following angles: in the branches with hetero-auxin, 20° down, 7° down and 5° down; in those without hetero-auxin, 15° up, 12° up and 10° up. Thus again hetero-auxin applied to the ends of decapitated branches acted instead of their young leaves in keeping them epinastic, though it did not keep them growing at the normal rate.

It may at first seem surprising that, in this species at least, hetero-auxin can act instead of developing leaves in keeping a branch epinastic, either when applied to the end of the branch if the branch has been decapitated, or, as was shown previously (1945), when applied to the main shoot if that has been decapitated. For this may make it seem that the hetero-auxin acts differently in a branch from what it does in a main shoot, which itself remains orthotropic. But it needs to be remembered that the hetero-auxin or natural auxin supplied from the end of a branch does not directly make the branch epinastic, but only makes it liable to be made or kept epinastic by the action of the main shoot tip. For if the main shoot tip is removed, the branches soon curve up and replace it. But the main shoot itself is dominant, and is not liable to correlative influences from other

shoots so long as it is dominant; and it therefore remains orthotropic although richly supplied with auxin. Indeed an abundant supply of auxin from its tip is the very thing which makes a shoot dominant, as is clear from earlier experiments by the writer (1931).

Although in the species so far investigated it has been shown that inhibition cannot travel up into a plagiotropic branch, or scarcely at all, yet it can penetrate a plagiotropic lateral bud. For in *Impatiens* and *Salvia* the lateral buds on a branch have been shown to be inhibited by the tip of that branch, and so also, as Massart (1924) showed, are the replacement buds on a branch of *Araucaria excelsa*, though not the buds destined to form the branches of the second order. This difference may perhaps be due simply to the difference in the length of the upward path, the inhibition being able to travel upwards for the short distance into a little lateral bud.

In any case, since inhibition does travel up into some plagiotropic buds, the freedom from inhibition, even at the earliest stages, of those other plagiotropic buds which develop into shoots of lower order than the shoots carrying them can hardly be due to an inability of inhibition to travel up into them. Such buds are formed by *Araucaria excelsa* and many tropical species, as was mentioned previously (1945, p. 115). Their freedom from inhibition seems to be a different phenomenon and probably connected with precocity. For it is apparently the rule that free buds are more precocious than inhibited replacement buds of the same species (see Sandt, 1925, p. 90). When the free buds have grown out into branches, then they may be expected to remain free from inhibition, since inhibition can scarcely travel up a plagiotropic branch.

This opportunity may be taken to mention that epinastism may be to some degree induced by the tip of the main shoot in leaves as well as in lateral shoots. For in *Stachys silvatica* it was several times noticed that a pair of leaves which had just emerged from the terminal bud but were still vertical, descended much less rapidly than usual to their normal positions if the terminal bud was cut off just above them.

SUMMARY

1. Correlative inhibition cannot travel up into plagiotropic branches of *Impatiens roylei* and *Salvia coccinea*, or scarcely at all, though it does travel down them, as was shown by Massart (1924) for *Araucaria excelsa* also.
2. In *Impatiens roylei* hetero-auxin in lanoline can act instead of developing leaves in keeping a branch epinastic and so plagiotropic, either when applied to the end of the branch if the branch has been decapitated, or when applied to the end of the main shoot if that has been decapitated.
3. In the light of these results the fact, shown previously (1945), that induction of epinastism and correlative inhibition tend to be alternative is further discussed. The freedom from inhibition of certain plagiotropic buds in other species is also discussed.

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A TEST OF SACHS'S THEORY OF THE PLAGIOTROPISM OF LAMINAE

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(With 5 figures in the text)

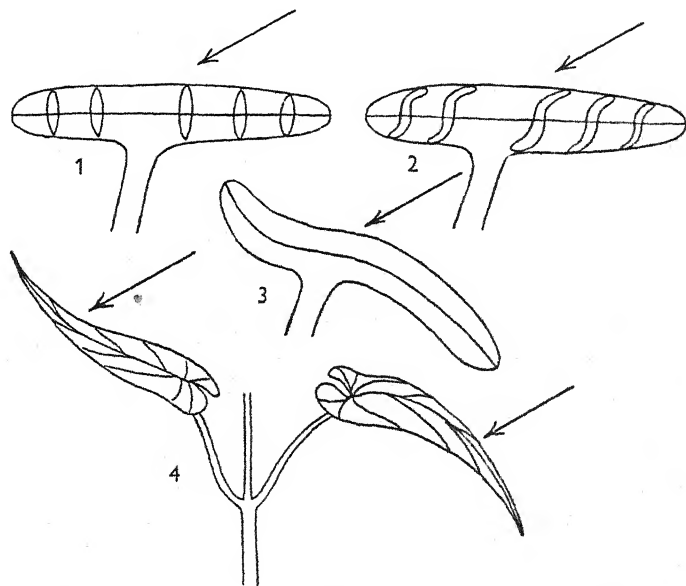
According to a suggestion of Sachs (1879, pp. 246 and 254) the movements of plagiotropic members of plants in general can be understood if these parts are thought of as built up of a number of narrow transverse orthotropic components standing in and parallel to the plane of dorsiventrality (Fig. 1). The morphologically upper ends of these components must be supposed to curve when stimulated like orthotropic stems, and their lower ends like orthotropic roots. The curvatures of the components will then bring about the observed curvature of the whole plagiotropic member (Figs. 2, 3). This suggestion was based on an earlier suggestion made by Stahl (quoted by Sachs, p. 252) with regard to lichens. It could be applied most simply to the movements of laminar organs, since in many lateral stems and petioles the normal orientation depends mainly or entirely on a balance between negative geotropism and epinastism.

Sachs indeed referred to his suggestion in one passage (p. 246) as a 'way of considering' (*Vorstellungsweise*). But whatever its nature may be and whatever the exact details, there is a simple way, which has apparently escaped notice, in which it can be tested by its consequences; and an experiment to test it on leaf blades of *Stachys silvatica* will be reported here. The question whether Sachs's suggestion is sound is clearly still a live one since, for example, Rawitscher (1932) has tried to explain the torsions starting from a similar idea.

The leaves of *S. silvatica* respond well to light, and in the usual manner. In overhead light the blades of the younger expanded leaves are about horizontal, and their petioles are inclined upwards at angles from 60 to 70°. If a plant is placed in a box open on one side, so that it receives the diffuse daylight from that side coming obliquely from above, the leaves curve as follows. In a leaf which is in front—that is, towards the open side of the box—with its tip towards the light (see Fig. 4), the petiole becomes dorso-convex and so sinks. The main part of the blade, between its tip and the petiole also curves dorso-convex, and the extreme basal part, the auricles, sometimes curves slightly dorso-concave, so that the whole blade makes an 'S' curve towards the light. In a leaf which is at the back with its tip away from the light these three parts all curve in the opposite senses and in the leaves which are in the lateral positions the petioles twist and the blades may also make 'S' curves towards the light in the transverse direction. The curvatures of the blades are rather slight, especially the dorso-concave curvatures, but they become stronger if the petioles are fixed. Also in *S. silvatica* the auricles are short and so do not curve much. Similar curvatures of blades in other species have been well described by Raydt (1925). It is necessary that very little light should strike the lower surfaces of the

leaves, especially of the 'back' leaves, since if more than a little light does so, it causes in all parts alike very strong dorso-convex curvatures which obliterate all the others. These last curvatures deserve further study.

The curvatures of the blades in response to light striking their upper faces obliquely can be interpreted on the basis of Sachs's theory. Thus, for example, in the main part of the blade of a leaf which is in front, with its tip towards the light, the transverse components, tending to turn their upper ends towards the light and their lower ends away, will tend to stretch the upper half of the blade and compress the lower half (see Figs. 1-3), and so may be supposed to make this part curve dorso-convex. But in the auricles of this leaf and in the main part of the opposite leaf with its tip away from the light the same



Figs. 1-3 illustrate Sachs's theory of plagiotropism. Fig. 1 shows the transverse components unstimulated; Fig. 2 shows them when stimulated by oblique light; Fig. 3 shows the resulting curvature of the lamina. The arrows show the direction of the light. Fig. 4 shows a pair of leaves of *Stachys silvatica* in oblique light. The serrations of their edges are omitted.

curvatures of the transverse components will compress the upper half and stretch the lower half, since these parts are attached at their ends nearer to the light; and so the curvatures of the components will tend to make these parts curve dorso-concave. Thus on Sachs's theory the sense in which any part of a blade curves must depend on the end at which it is attached.

In order to find out whether this is so, the following experiment was performed (see Fig. 5). From the median parts of the blades of young recently expanded leaves of plants of *S. silvatica*, when the blades had just descended to the horizontal position, flaps were cut out by two cuts parallel to the mid-rib and a third transverse cut through the mid-rib near its basal end. At their apical ends the flaps remained attached to the rest of the blade. They were mostly from 3 to 4 cm. long and from 2 to 3 cm. wide and each was supported on a thread near its free end. The petioles were fixed in position at their distal ends, and

the plants, which had been growing in overhead light in a greenhouse, were placed in boxes lined with black paper and open on one side towards the north, so that the leaves operated upon were either in front with their tips towards the light, or behind with their tips away from it.

Through this operation the parts of the blades forming the flaps were now attached only at their far ends, and consequently on Sachs's theory they should curve in response to the light in the sense opposite to the normal, if at all. The actual changes of curvature are shown in the table. Some of the leaves, nos. 4-6 of the front leaves and nos. 4 and 5 of the back leaves, had all their apical parts beyond the flaps lightly held between two microscope slides clamped at their far ends, as is shown in Fig. 5. The purpose of this arrangement was to provide a firmer attachment against which the strips

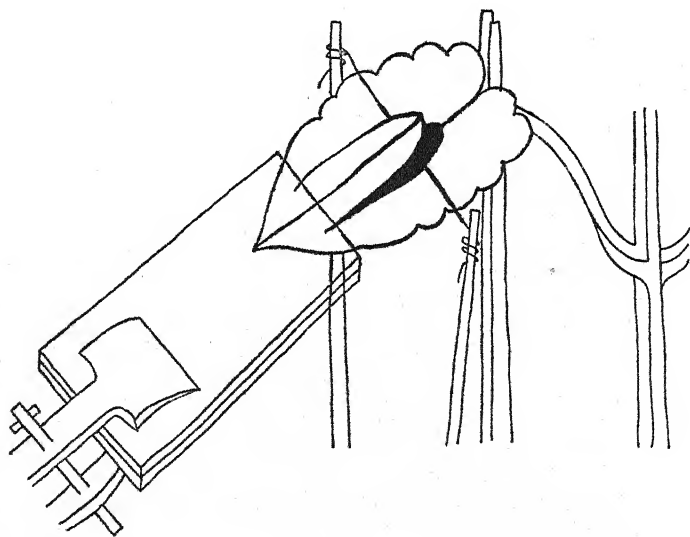


Fig. 5. A leaf of *Stachys silvatica* with a distally attached flap cut out from it and supported on a thread, and with the apical part of the leaf held between glass slides.

might react: but actually it was not found to alter the result, and so was soon given up. Those leaves which were not held between slides were supported on rough black paper instead, except front leaf no. 1, which was supported on threads.

The duration of the experiment was about 31 hr. for most of the leaves, but from 48 to 54 hr. for front leaves nos. 1 and 4, and back leaf no. 3. After 31 hr. the curvatures usually did not change any more. The curvatures of the flaps were taken to be the curvatures of their mid-ribs. They were measured well before the evening sleep movement began. The experiments were made on only one leaf of each plant at a time, so that this leaf might always be at about the same distance from the open side of the box.

Table 1 shows that in the front leaves the flaps all curved dorso-convex, just as do the corresponding parts of intact leaves, though on Sachs's theory they should have curved dorso-concave if at all. Also all except one of the flaps of the back leaves, which on that theory should have curved dorso-convex, curved either dorso-concave or scarcely at all. It need not cause surprise that they often failed to curve at all, since even in intact

leaves the dorso-concave curvatures are often feeble. A few similar experiments with leaves of *Lunaria biennis* gave similar results.

Sachs's theory therefore does not hold for the phototropic curvatures of these leaf blades, and probably not for the very similar curvatures of those of other species either, though possibly it might be found to hold for such different objects as the thallus lobes of liverworts with which he experimented. It therefore needs to be considered what empirical rule would indicate correctly the senses of the phototropic curvatures of leaf blades in different conditions. If the region of attachment of a blade to its petiole may be called its centre, though not geometrically so, the rule appears to be that light striking

Table 1. *Stachys silvatica*. Changes of curvature in degrees of distally attached flaps of leaf blades in oblique light from above. Changes of curvature towards increased dorso-concavity or decreased dorso-convexity are recorded as positive

Leaf no.	Front leaves		Leaf no.	Back leaves	
	Curvature at start	Change of curvature		Curvature at start	Change of curvature
1	Dorso-convex 25%	-15	1	Dorso-convex 10%	0
2	— 0	-15	2	" 5	-10
3	Dorso-convex 10	-15	3	" 20	+10
4	" 12	-11	4	" 10	-2
5	" 3	-17	5	" 20	0
6	" 8	-10	6	Dorso-concave 13	+7
7	" 8	-15	7	" 10	0
8	Dorso-concave 10	-20	8	" 10	0
9	" 15	-15	9	Dorso-convex 7	+25
			10	" 10	+30
	Mean	-15		Mean	+6

obliquely the upper face of a blade tends to make the parts of it which it strikes centripetally to curve dorso-convex, and those which it strikes centrifugally to curve dorso-concave. This rule is further supported by the observation that in *Stachys silvatica* and other species the curvatures, both convex and concave, induced in the leaf blades by oblique light from above are commonly made not only in the direction of the light, but also to some degree in the transverse direction. On Sachs's theory this would not be expected.

SUMMARY

1. From Sachs's theory that the plagiotropism of a lamina may be regarded as depending on the curvatures of orthotropic transverse components within it, it would follow that the sense in which any part of a lamina curves, whether dorso-convex or dorso-concave, must depend on whether that part is attached by the end towards the stimulus or away from it.

2. It is shown by a phototropic experiment that in leaf blades of *Stachys silvatica* this is not so, and an empirical rule for the senses of the curvatures of different parts of such blades is proposed as an alternative.

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TUSsock FORMATION IN *AMMOPHILA* *ARENARIA* (L.) LINK.

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INTRODUCTION

The observations to be considered here were made on *Ammophila arenaria* in a sand-dune system at Luskentyre on the west coast of the Isle of Harris, Outer Hebrides. The system occupies a small rounded promontory about half a mile broad and quarter of a mile long, facing west and exposed to strong winds although sheltered to some extent from the full force of Atlantic gales by the Island of Taransay. The sand is highly calcareous, consisting largely of finely comminuted shell fragments. *Ammophila arenaria* is the chief binding agent, *Agropyron junceum* (L.) Beauv. playing only a very subsidiary role in the earlier stages of the succession. A full account of the vegetation will be given elsewhere.

It must be emphasized that the results obtained are only applicable to the community studied, although further study may lead to their more general application.

In the majority of tussock-forming grasses the typical habit results from the morphology of the plant. Even under unfavourable conditions the potential ability to form tussocks is evident from the presence of localized groups of buds and shoots, and more favourable conditions are reflected only in the increased size and vigour of the tussocks. *Ammophila arenaria* is an exception to this generalization. In passing from foreshore to fixed dune four types of habit can be seen: (1) In the foreshore community the *Ammophila* population consists mainly of young plants which have not yet formed a rhizome, although occasionally plants bearing one or two rhizomes of 6 ft. or less have been found. These are generally evident before excavation from the small groups of leaves ('Leafy Shoots', see below) arranged in more or less straight lines. (2) The mobile dunes have what appears to be a uniform cover of *Ammophila*, but closer examination shows considerable variation in density though there are no evident tussocks. (3) With the entry of other species in quantity and the resultant partial stabilization of the sand surface, the *Ammophila* assumes a markedly tussocky habit. In the early stages of fixation there are large tussocks of *Ammophila* up to 12 in. in height (exclusive of the aerial parts) with few shoots dead or alive between them. (4) The final stage of fully fixed dune with closed vegetation cover is sharply demarcated from the earlier stages, and is probably only reached where there is shelter from the full force of the wind. Here *Ammophila* occurs as isolated shoots uniformly distributed. Our acquaintance with sand dunes elsewhere, and examination of the literature (Tansley, 1939, etc.) suggests that such variation in habit is widespread, though the tussocks often do not build up to such a height. This variable behaviour suggests that tussock formation is not an inherent property of the plant but occurs incidentally as a response to environmental conditions. In fact it is found that

tussocks may be formed from parts of several plants and a more accurate description would be extreme over-dispersion of the vertical leafy shoots.

MORPHOLOGY

At a fairly early stage in the life of an *Ammophila* seedling (probably in the first year though this has not been definitely established) it produces one or more rhizomes which grow horizontally beneath the sand surface. The internodes of the rhizome vary from 0.1 to 8.0 in. in length. Each node bears a single colourless leaf about 6 in. long. In older parts of the rhizome these leaves are lacking, having decayed or possibly been removed by the friction of the very mobile sand. The axillary buds in all plants examined remain alive though generally dormant, as long as the rhizome bearing them remains alive. If the buds develop, and only a minority do so, they may form branches similar in all respects to the parent rhizome except that the first one to four internodes are very short (a typical value is 0.2 in. for the first four internodes together followed by one of 4.5 in.), or they may produce vertical shoots, here referred to as 'leafy shoots'. The latter reach to the surface and are characterized by profuse branching and numerous short internodes, though if the point of origin is far below the surface some of the lower internodes may be 4 or 5 in. long. These two types of branch are distinct although occasionally rhizome branches may turn up and become leafy shoots. Leafy shoots may continue to live after the rhizome from which they are derived has died (all nodes readily form adventitious roots) and it is to them that the plant owes its ability to grow up through accumulated masses of sand. The so-called tussocks are localized groups of leafy shoots around which wind-blown sand has accumulated, and the problem of their origin is that of the origin of the groups of leafy shoots.

METHOD

A considerable number of plants or portions of plants were excavated and eight used for detailed examination and measurement. In the course of dune fixation the rhizome becomes separated into comparatively short lengths by the death of the older parts and many of the leafy shoots become detached from the rhizome, so that such plants are unsuitable for analysis. Seven of those for which measurements are given were taken from the mobile dunes where localization, though present, is not so marked. The eighth plant, E, was from the foreshore. The procedure was to take a leafy shoot from the side of a dune and dig down to the rhizome from which it was derived. The latter and all branches exposed were followed to their apices and backwards as far as possible. It proved impossible to excavate whole plants as the rhizomes came horizontally from under the dunes. On each rhizome the internodes were measured and the occurrence of branches and leafy shoots noted. The measurements made are given in Table 1 and summarized in Table 2.* The individual plants are designated A, B, C, etc., and the branches as follows:

- F, etc. The oldest rhizome exposed.
- F₃, etc. First order branches.
- F_{3b}, etc. Second order branches.
- F_{3b} 1, etc. Third order branches.

Throughout this paper a leafy shoot or branch is taken as arising from the internode preceding the node which actually bears it. Such terminology makes discussion of the data simpler.

* In calculating means, etc. the initial short internodes of branches are omitted.

Table 1. Internode length (in.) and leafy shoot occurrence

PLANT A	PLANT C	4.0	5.6	1.0	5.4
2.7	3.7	Apex	6.3 LS	2.8	6.1
4.0	5.0		3.3	5.3	5.8 LS
3.7	5.0	br 3	5.9 br 1b	6.3 br 3b 1	4.7 LS
2.9	4.3 br 1	0.3	2.5 br 1c	7.1	4.1 LS
1.8	4.9	4.7	(broken)	1.8	4.1 LS
1.9	5.1	4.2	1.2 LS	2.0	3.8 LS
2.4	6.0	5.1 LS	Apex	Died	4.2 LS
2.6	4.8	5.0 LS			4.4
2.2	5.0	4.7	br 1a	br 3b 1	4.8
2.1	5.7	4.3	0.2 (3 nodes)	0.2 (2 nodes)	1.1
2.1	6.3 br 2	Broken	5.4	2.0	2.0
2.0	6.2 br 3		4.2	3.5 LS	4.4
2.1	5.5 LS	PLANT D	Died	1.9	4.1
3.0 LS	6.5 LS	0.7		Apex	4.0
3.9 LS	7.0 LS	1.0	br 1b		3.3
6.0 LS	5.7 LS	6.2	0.1	br 4	Apex
6.5 LS	5.6 LS	8.0	0.1	0.2 (3 nodes)	
2.9 LS	6.2 LS	7.2	1.4	1.4 br 4a	PLANT H
1.7 LS	5.0 LS	7.3	0.2	1.0 (dead br)	1.4
2.9	4.5 LS	6.8	1.8	0.5	4.4
3.4 LS	4.7	5.9 LS	3.3	0.7	6.3
2.5 LS	4.1 LS	5.9 LS	2.7	Apex	4.5
Apex	2.6 LS	5.2 LS	1.1		4.5
	2.9 new br	6.3 LS	0.2	br 4a	4.8
	4.0	5.4 LS	Apex	0.2 (3 nodes)	4.5
PLANT B	3.7	4.9 LS		0.4	4.7 br 1
4.3 LS	3.2	4.5	br 2	0.5	5.6 LS
3.1	3.4	4.9	0.2 (3 nodes)	0.6	6.1
3.7 LS	2.2	4.8	2.3 LS	3.9	4.8
4.6	1.9	3.3	2.9	2.8	1.0
4.5 LS	3.2	1.6	3.1	2.4 LS	3.9
4.7 br 1	2.1	3.5	Broken	Apex	6.2 br 2
5.7 br 2	2.6	3.3			2.5
6.2	3.7	3.7	br 3	PLANT G	0.7
6.2	3.0	3.8	0.2 (3 nodes)	1.8	1.3
5.0	2.8	4.1	0.2 br 3a	2.5	3.2 LS
6.0 LS	Apex	4.5	3.5	3.6	4.7 LS
7.0 LS		4.7	3.9 br 3b	4.9	5.4 LS
5.0 LS	br 1	3.2	1.4	5.3	6.0
Apex	0.2 (3 nodes)	Apex	3.1	4.3	4.9 LS
	1.0		3.2	4.4	3.5 LS
br 1	1.5	PLANT E	1.9	5.5	3.4
0.1	3.0	1.4 LS	4.4	6.1	3.1 LS
0.1	4.0	2.4 LS	5.2	5.8 br 1	Apex
4.2	6.0	3.8 LS	6.0	4.2	
4.6	6.4	2.4 LS	6.5	4.7	br 1
6.4	3.0 LS	3.0 LS	4.0 LS	5.5	0.3 (4 nodes)
5.6	2.0 LS	5.0 LS	2.2 LS	7.0	1.7
4.2	0.7	5.2 LS	Apex	5.7	2.8
4.0	Broken	4.0 LS		5.0	2.4
3.3		4.8	br 3a	5.5	3.5
2.7 LS	br 2	5.2	0.2 (4 nodes)	5.8 LS	4.4
2.7 LS	0.2	5.1	2.3	6.2	3.6
3.0 LS	2.1	4.6 LS	3.8	5.6	2.3
3.0 LS	4.6	3.9	4.8	5.5	2.6 LS
1.7 LS	6.2	3.9	6.4	4.5	Apex
2.4 LS	7.7 LS	Apex	5.2	2.9	
4.6 LS	8.0 LS		4.3	4.1	br 2
5.6 LS	7.2 LS	PLANT F	3.7	4.9	0.2 (2 nodes)
5.7 LS	6.7 LS	2.8	4.9 LS	5.1	0.4
5.0 LS	6.0	4.7 br 1	5.2	5.0	4.3
2.5 LS	5.8	5.7 br 2	4.4	5.3	2.5
0.4 LS	5.0	5.6 br 3	4.1 LS	6.2 LS	3.7
Apex	4.8	5.0 br 4	3.6 LS	Apex	4.1
	2.6	4.6	3.8 LS		2.9
br 2	4.3	Broken	3.5 LS	br 1	1.2
0.2	3.0		1.3	0.2 (2 nodes)	2.8
5.7	2.8	br 1	Apex	1.3	4.8
5.2 LS	3.2	0.2 (4 nodes)		4.2	4.7
6.5 LS	3.7	0.5	br 3b	4.9	3.6
6.5 LS	3.8	1.8	0.2 (3 nodes)	5.1	4.0
Died	3.3	5.0 br 1a	0.7	5.4	Apex

Table 2

Plant	A	B	B ₁	B ₂	C	C ₁	C ₂	C ₃	D
Total length	65.3	66.0	71.6	23.9	158.1	27.6	98.1	28.0	120.7
No. of internodes	22	13	19	4	36	9	21	6	26
Mean length of internode	2.968	5.077	3.768	5.975	4.392	3.067	4.671	4.667	4.642
S.E.M.	0.267	0.306	0.357	0.320	0.232	0.688	0.383	0.158	0.364
No. of leafy shoots	8	6	12	3	10	2	4	2	6
Mean length of internode before leafy shoot	3.737	5.083	3.275	6.067	5.270	2.500	7.400	5.050	5.600
No. of extrema	8	6	5	1	18	1	6	2	10
P	0.99	0.72	>0.99	0.42	0.95	>0.99	>0.99	0.59	>0.99
No. of branches	—	2	—	—	4	—	—	—	—
Mean length of internode before branch	—	5.200	—	—	4.925	—	—	—	—
% L.S. internodes	36.36	46.15	63.16	75.00	27.78	22.22	19.05	33.33	23.08
	E*	F	F ₁	F _{1a}	F _{1b}	F ₂	F ₃	F _{3a}	F _{3b}
Total length	54.7	28.4	32.1	9.6	10.7	8.3	50.2	61.3	27.0
No. of internodes	14	6	9	2	7	3	14	15	8
Mean length of internode	3.907	4.733	3.567	4.800	1.529	2.767	3.586	4.087	3.375
S.E.M.	0.322	0.429	0.731	0.600	0.445	0.242	0.472	0.316	0.883
No. of leafy shoots	9	—	2	—	—	1	2	5	—
Mean length of internode before leafy shoot	3.533	—	3.750	—	—	2.300	3.100	3.980	—
No. of extrema	5	1	3	—	2	—	5	5	2
P	0.96	0.91	0.85	—	0.81	—	0.96	0.98	0.93
No. of branches	—	4	3	—	—	—	2	—	1
Mean length of internode before branch	—	5.250	4.467	—	—	—	2.050	—	6.300
% L.S. internodes	64.29	—	22.22	—	—	33.33	14.29	33.33	—
	F _{3b1}	F ₄	F _{4a}	G	G ₁	H	H ₁	H ₂	All plants
Total length	7.4	3.6	10.6	142.9	87.2	101.4	23.3	39.0	1357.0
No. of internodes	3	4	6	29	21	25	8	12	342
Mean length of internode	2.467	0.900	1.767	4.928	4.152	4.056	2.912	3.250	3.968
S.E.M.	0.518	0.196	0.601	0.213	0.203	0.330	0.306	0.393	0.090
No. of leafy shoots	1	—	1	2	6	7	1	—	90
Mean length of internode before leafy shoot	3.500	—	2.400	6.000	4.450	4.343	2.600	—	4.380 (S.E.M. 0.171)
No. of extrema	1	1	1	10	5	9	4	6	—
P	—	0.42	0.91	>0.99	>0.99	>0.99	0.32	0.56	—
No. of branches	—	2	—	1	—	2	—	—	21
Mean length of internode before branch	—	1.200	—	5.800	—	5.450	—	—	4.381 (S.E.M. 0.452)
									(omitting F ₄) 4.716 (S.E.M. 0.430)
% L.S. internodes	33.33	—	16.67	6.90	28.57	28.00	12.50	—	26.32

Internodes bearing neither leafy shoot nor branch: number, 231; mean length, 3.770; S.E.M., 0.106.

* From foreshore community.

VARIATION OF LENGTH OF INTERNODE

Table 2 shows a considerable variation in the mean length of internode in the various branches from 1.529 to 5.077 in. (F4 with a mean length of 0.900 in. and B2 with mean length of 5.975 are both short branches with only four internodes and may be disregarded). There is little evidence that this variation is connected with position of the branch on the plant though it must be emphasized that all the rhizomes examined, except plant E from the foreshore community, are from old well-established plants. It is possible that branches produced from young plants might have a mean internode length uniformly and significantly different from that of the branches produced from older plants.

It can be seen from Table 1 that there is a tendency for the internode length along an individual branch to vary cyclically (i.e. to show an alternation of maximum and minimum values). The number of extrema per branch is shown in Table 2. (In a set of values $X_1, X_2, X_3, \dots, X_n, \dots, X_n$ is an extremum when its neighbours X_{n-1} and X_{n+1} are both greater or less than X_n .) The corresponding values for P represent the probability that such a series of values would have more than that number of extrema by chance, i.e. that the cyclic variation is real (Gleissberg, 1946*a, b*). From the table it will be seen that of the thirteen branches of more than ten internodes, eleven show a value for P of 0.05 or over, i.e. taking a 5% level of significance there is strong evidence of cyclic variation.

From the data an estimate of the length of the cycle can be made. Omitting branches with only one extremum and internodes beyond the end extrema in other branches the following values are obtained:

No. of internodes, 200.

No. of extrema, 93.

These give a value of 2.15 for the ratio: no. of internodes/no. of extrema, i.e. a mean cycle length of 4.3 internodes. It is likely that the true value is greater than this, as occurrence of extrema by chance will lower the apparent cycle length.

The cause of this cyclic variation is unknown. It is possibly an annual one, but there is no evidence either way.

OCCURRENCE OF LEAFY SHOOTS ON THE RHIZOME

Table 3 shows that the mean length of internodes bearing leafy shoots is significantly greater than that of all internodes. As the mean internode length of different individual branches varies considerably this difference could be accounted for if leafy shoots arose more abundantly on branches whose internodes have a mean length greater than the

Table 3. *Comparison of internode lengths*

Comparison*	Difference	s_d	n	t	P
L-A	0.412	0.19718	341	2.089	0.02-0.05
L-N	0.610	0.20057	319	3.041	0.001-0.01
B-N	0.611	0.37683	250	1.621	0.1-0.2
Br-A	0.748	0.39230	342	1.907	0.05-0.1
Br-N	0.946	0.38975	248	2.427	0.01-0.02
Br-L	0.336	0.42047	107	0.799	0.4-0.5

* L, internodes bearing leafy shoots; B, internodes bearing branches; Br, internodes bearing branches (less F4); N, internodes bearing neither leafy shoots nor branches; A, all internodes.

mean length of internodes on all branches examined. Calculation of the appropriate regression shows that this is not so (Table 4).

Table 4. *Regression of percentage of internodes with leafy shoots on mean length of internode in branches with more than ten nodes*

<i>b</i>	<i>s_b</i>	<i>t</i>	<i>P</i>
-1.1116	9.2065	0.1207	>0.9

Examination of Table 1 shows that not only do leafy shoots tend to arise from groups of consecutive internodes but the groups themselves tend to occur together. The association of leafy shoot internodes into groups and the mean internode length of such groups is shown in Table 5. The frequency of large groups is greater than would be expected by

Table 5

No. of consecutive nodes bearing leafy shoots	1	2	3	4	6	8	12
Observed frequency	15	6	3	2	3	2	1
*Expected frequency of groups (to nearest 0.1)	48.9	12.9	3.4	0.9	0.1	0	0
Total number of leafy shoots	15	12	9	8	18	16	12
Mean length of internode	4.067	3.525	5.500	5.575	4.683	4.575	3.275
<i>d</i> (difference from mean length of all internodes)	+0.099	-0.443	+1.532	+1.607	+0.715	+0.607	-0.693
<i>s_d</i>	0.43909	0.48888	0.56205	0.59532	0.40249	0.42567	0.48888
<i>n</i>	341	341	341	341	341	341	341
<i>t</i>	0.225	0.906	2.726	2.699	1.776	1.426	1.418
<i>P</i>	0.8-0.9	0.3-0.4	0.001-0.01	0.001-0.01	0.05-0.1	0.1-0.2	0.1-0.2

* Calculated from $(280/342)^2 \times (90/342)^r \times 342$ for a group of *r* nodes.

chance. It will be seen that the mean internode length in groups of 1, 2, 8 and 12 consecutive leafy shoot internodes does not differ significantly from that of all internodes, but that the mean internode length of groups of 3 and 4, and possibly of 6 such internodes is significantly greater than that of all internodes. It should be noted that as the number of consecutive internodes increases beyond the cycle length the mean internode length must approach that of all internodes.

DISCUSSION

These facts may be accounted for by the following hypothesis which, although based on no experimental evidence, is put forward as the most probable explanation. It is assumed first that all buds are capable of forming leafy shoots. Since the majority remain dormant it must further be assumed that an external stimulus is required to initiate the growth mechanism. Initially a bud stimulated to grow must derive its food supply primarily from the internode immediately preceding it, and secondarily from adjacent internodes.

If a leafy shoot arises from a short internode the food supply in that internode may well be insufficient and adjacent internodes will be drawn on with their subsequent depletion. Since internode length varies cyclically the latter will in most cases be short also and

exhaustion of the rhizome will result, preventing response to the stimulus in the adjacent buds. If, on the other hand, the leafy shoot arises from a long internode, the food supply in the latter will be more than sufficient, and since the adjoining internodes will also be long, there will be a greater likelihood of adjacent buds responding to stimulus and a group of leafy shoots arising.

Once a leafy shoot has reached the surface and started to photosynthesize it will enhance rather than deplete the adjacent rhizome reserves, so that further buds even on short internodes may commence growth provided the stimulus is still present. Leafy shoots at the end of large groups were found to be shorter, suggesting a later commencement of growth; no detailed measurements are available.

The postulation of an external factor is not pure hypothesis, for in the field it was obvious that parallel, but unconnected, rhizomes growing in the same area of sand produced leafy shoots within, and only within, the same limited area. The mode of formation of tussocks from a number of rhizomes crossing the same area of stimulation will be apparent.

OCCURRENCE OF BRANCHES ON THE RHIZOME

The production of branches raises similar problems to that of leafy shoots, and further poses the question why a bud gives rise to a branch rather than a leafy shoot and vice versa. There is some indication (see Table 3) that internodes giving rise to branches have a higher mean length than that of all internodes but the data is too scanty to enable any conclusions to be drawn.

SUMMARY

An account is given of the behaviour of *Ammophila* in a dune system on the Isle of Harris, Outer Hebrides.

'Tussocks' are formed only on the older dunes, and are aggregations of aerial shoots rather than true tussocks.

The length of internode varies cyclically along the rhizome.

Buds on the rhizome may remain dormant or may produce either further horizontal branches or vertical aerial shoots (leafy shoots). The occurrence of the latter is considered in detail. It is suggested that an external stimulus is necessary for the development of buds.

Groups of consecutive internodes bear leafy shoots more frequently than would be expected by chance. Groups of 3-6 such internodes have a greater mean length than that of all internodes.

It is suggested that only where the internodes are long are there sufficient food reserves in the rhizome for a group of adjacent buds to develop.

Groups of leafy shoots on one rhizome or several adjacent rhizomes give rise to tussocks.

This work was partly financed by a grant from the Ernest and Evelyn Weiss Botanical Travel Fund of the University of Manchester.

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ASTOMELLA, A NEW MEMBER OF THE PERISPORIALES

By M. J. THIRUMALACHAR

(With Plate 6 and 7 figures in the text)

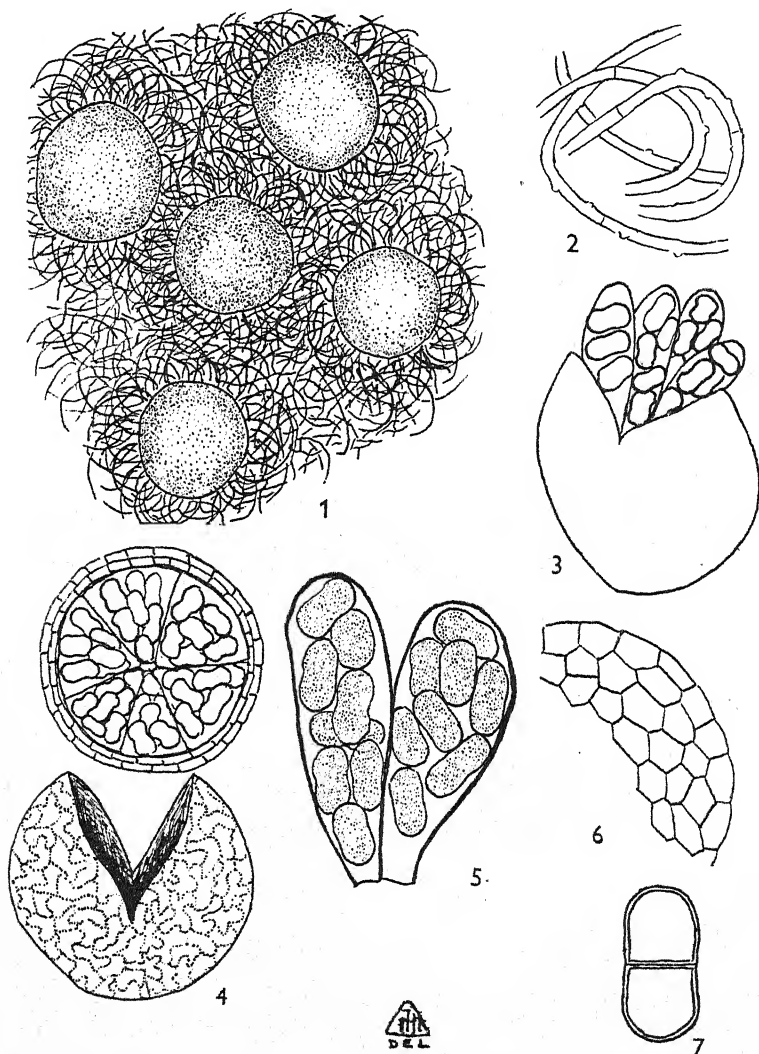
An ascomycetous fungus collected on the leaves of *Neolitsea zeylanica* in Nandi Hills, Mysore, proved on examination to be of unusual interest, having characters quite different from those of any other fungus so far described. The fungus is hypophyllous and superficial, the closely interwoven cinnamon-yellow hyphae (Pl. 6, fig. 1) forming a dense woolly mass of covering on the surface of the leaves. In early stages of infection, the fungus forms small cinnamon-brown patches on the lower surface of the leaves, and as development proceeds these coalesce with one another. In later stages the perithecia are seen embedded within the hyphal mass, appearing as tiny reddish black specks. After the completion of the production of the perithecia the felt of mycelium begins to peel off as thin crusts.

Sections through the leaves indicate that the fungus forms a basal substratum of creeping hyphae, from which erect circinate branches are formed in large numbers, thus producing a heterotrichous habit. The epidermal cells of the host are penetrated by haustorial processes formed by the hyphal strands. The felt of mycelium is so delicately attached to the host that it is very difficult to demonstrate the penetration of the fungus within the host, especially in later stages, when the entire felt of mycelium begins to peel away from the host. In very early stages, when the mycelium is arachnoid creeping on the leaf surface, the penetration into the epidermal cells and the consequent depletion of their cell contents have been observed. In fact, the presence of the fungal patches on the lower surface of the leaves is clearly indicated by the discoloration of the host in corresponding places on the upper surface. This confirms the parasitic nature of the fungus, which in its mode of parasitism resembles to a very great extent the ectoparasitic alga, *Cephaleuros mycoidea* Karst.

The mycelium is septate, cinnamon-yellow, creeping on the surface of the leaves and sending in haustorial processes into the epidermis. There are no hyphopodia so characteristic of many of the Perisporiaceae, but circinate erect branches which could be compared morphologically with setae are present in large numbers. The hyphae are not uniformly broad, but develop here and there numerous nodular or hemispherical bulges (Text-fig. 2).

The perithecia are found embedded within the hyphal felt, appearing macroscopically as tiny globular bodies. They can be collected in abundance in the months between November and February, after which they are either absent or completely empty. Mature perithecia are reddish brown, subglobose to spherical, 140-180 μ in diameter and smooth. They do not possess any appendages, nor have they any ostiole or any similar structure for the escape of the ascospores. The perithecia are therefore astomous and cleistocarpous. The wall of the perithecium is composed of two distinct layers. The outer one is reddish brown, one-layered, hard and circumscissile. It appears to be composed of septate meandering hyphae (Text-fig. 4). The inner wall is also one-layered

though in optical sectional view it appears to be two- to three-layered (Text-fig. 4), and is composed of polygonal cells. This inner hyaline layer is comparable both in structure and development with the peridial layer described by Gäumann (1922) in *Lanomyces tjibodensis* Gäum. from Java.



Text-fig. 1. Showing the mycelium with perithecia. $\times 200$.

Text-fig. 2. Septate hyphae with hemispherical bulges. $\times 1500$.

Text-fig. 3. Showing the umbellate cluster of asci. $\times 400$.

Text-fig. 4. Dehiscence of the perithecium. $\times 400$.

Text-fig. 5. Ascus showing the biseriate arrangement of the spores. $\times 800$.

Text-fig. 6. Portion of the inner hyaline wall layer showing the parenchymatous cells. $\times 800$.

Text-fig. 7. Mature ascospore showing 1-septate condition. $\times 1500$.

The asci are from four to ten in number, developed in a basal umbellate cluster. Consequently in the development and disposition of the asci it differs considerably from the members of the Eurotiaceae where the asci are scattered irregularly and very rarely

grouped in corymboid clusters. Mature asci are clavate to obovate, hyaline, and are attached at the base. The ascospores are eight in number, pale cinnamon-yellow in colour and uniseptate. They are rounded at both ends, slightly constricted at the septa, smooth (Text-fig. 7) and measuring $22-30 \times 11-14 \mu$. The spores within the ascus are arranged biserially. Considerable difficulty was experienced in securing mature perithecia with fully developed ascospores, as most of the perithecia were found to be either empty or containing only immature asci. Consequently, large collections of the material with perithecia in all stages of development were examined carefully from time to time. It became evident that as the perithecia approached maturity the asci and ascospores along with the inner wall layer were forcibly ejected after a bivalvular cracking of the perithecium. Some ripe perithecia that were examined under the low power of the microscope suddenly ejected the asci with the ascospores, all of which were still enclosed within the inner wall when just teased with a needle (Text-fig. 4). The ascospores at this stage are still in the process of development, the septation within them not having taken place. It therefore seems probable that the dispersal of the asci with the ascospores takes place just before the complete ripening of the latter. This probably explains the scarcity of the mature ascospores.

The superficial mycelia forming a woolly felt-like covering on the surface of the leaves with perithecia embedded within them, recalls the condition present in the genera *Cryptothecium* Penz. & Sacc. and *Lanomyces* Gäm. In *Cryptothecium javanicum* Penz. & Sacc. (Penzig & Saccardo, 1897), described from Java on *Elettaria*, the perithecia were found on decaying leaves and were stated to be astomous and possessing amerospores which were 6- to 8-guttulate. The fungus was collected again in the same locality by von Höhnelt in Java on the same substratum, which, however, was identified as *Anomum* and not *Elettaria*. The perithecia, according to v. Höhnelt (1909), are not, however, astomous, but possess a small ostiole with distinct radiating periphyses. v. Höhnelt concluded, therefore, that it was a member of the Nectriaceae. The plasma of the ascospores showed slender divisions into four or sometimes six parts, and he regarded the species as belonging to the genus *Calonectria*. Since no definite septations were noticed in the ascospores and to meet correct descriptions of the 1-celled state, he also named the fungus as *Byssonectria javanica* (Benz. & Sacc.) Höhnelt. Since *Cryptothecium* is now regarded as a synonym of *Byssonectria* or *Calonectria* (according to Clements & Shear (1931)), the present fungus on *Neolitsea zeylanica* cannot be identified with that genus.

Lanomyces tjibodensis, described by Gämman (1922) in Java, possesses similar felt-like mycelium with erect, circinate branches. The mycelium, however, is intramatrical to start with, emerging and becoming superficial later. The perithecia are borne on the superficial mycelium which is simple and exhyphopodiate. They are astomous, but each possesses a single ascus containing numerous (more than eight) 1-celled ascospores. In the present fungus, however, there are 6-10 asci with 2-celled ascospores. As the fungus under study differs in essential features from all other genera of fungi so far known, the writer proposes to accommodate it in a new genus under the Perisporiales. The name *Astomella* is proposed.

***Astomella* Thirumalachar gen. nov.**

Mycelium superficiale, processibus haustoriis in epidermate praeditum, lanosum, cinnamomeo-brunneum. Perithecia superficialia, in hypharum massa insidentia, globosa, luteo-brunnea, astomata; integumentum duplex, pariete exteriori rubro-brunneo ex

hyphis vagantibus composito, interiore vero hyalino, parenchymatico. Asci 6-10, paraphysati, 8-spori; sporae uniseptatae; asci cum pariete interiore in maturitate vehementer expelluntur.

Species typica *Astomella Neolitseae* Thirumalachar.

Mycelium superficial with haustorial processes within the epidermis, woolly, cinnamon-brown. Perithecia superficial, buried in the hyphal mass, globose, yellowish brown, astomous, with two distinct wall layers; outer reddish brown, formed by septate meandering hyphae, inner hyaline, 1-layered and parenchymatous. Asci 6-10, paraphysate, 8-spored; spores 1-septate; asci along with inner wall forcibly ejected at maturity.

Type species *Astomella Neolitseae* Thirumalachar.

Astomella Neolitseae Thirumalachar sp. nov.

Fungus hypophyllus, pallide luteus, maculas in facie superiore foliorum efficiens; mycelium superficiale, initio arachnoideum, postea cinnamomeo-brunneum atque lanuginosum, haustoriis in epidermate evolutis, ramis circinatis setae similibus. Perithecia superficialia, globosa ad subglobosa, luteo-brunnea, astomata atque cleistocarpa, 140-180 μ diam.; perithecii integumentum duplex, pariete exteriori rubro-brunneo, ex hyphis septatis vagantibus composito, duro, in maturitate fissione bivalvata dehiscente; pariete interiore hyalino, parenchymatico, cellulis rectangularibus vel polygonalibus. Asci 6-10, clavati vel obovales, in acervo umbellato dispositi, paraphysati, 8-spori, magnitudinis 87-112 \times 35-45 μ . Sporae ovatae, uniseriatae, biseriatim dispositae, cinnamomeo-luteae, utrinque rotundatae, ad septa paullo constrictae, laeves, magnitudinis 22-30 \times 11-14 μ . Asci atque sporae simul cum pariete interiore in maturitate vehementer expelluntur.

Habitat in foliis *Neolitsea zeylanicae*, Nandi Hills, Mysore, 14. x. 1944, leg. M. J. Thirumalachar. Typus positus in Herb. Crypt. Ind. Orient., New Delhi, et in Herb. I.M.I., Kew, Anglia.

Hypophyllous, causing pale yellowish patches on the upper surface, mycelium superficial, arachnoid in the beginning and cinnamon-brown and woolly later on, developing haustoria within the epidermis, with circinate setae-like branches. Perithecia superficial globose to subglobose, yellowish brown, astomate and cleistocarpous, 140-180 μ in diameter with two-layered wall; outer reddish brown, formed by the septate meandering hyphae, hard, opening at maturity by bivalvular split; inner hyaline, one-layered and parenchymatous, cells rectangular to polygonal. Asci 6-10, clavate to obovate, arranged in umbellate cluster, paraphysate measuring 87-112 \times 35-45 μ , 8-spored. Spores ovate, 1-septate, biseriately arranged, cinnamon-yellow, rounded at both ends, slightly constricted at the septa, smooth and measuring 22-30 \times 11-14 μ . Asci and spores along with the inner wall layer ejected forcibly at maturity.

Habitat on the leaves of *Neolitsea zeylanica*, Nandi Hills, Mysore, 14. x. 1944, leg. M. J. Thirumalachar. Type deposited in the Herb. Crypt. Ind. Orient., New Delhi, and in Herb. I.M.I., Kew, England.

In the possession of superficial mycelia bearing globose astomous perithecia, the genus *Astomella* has characters in common with the members of Eurotiaceae, Erysiphaceae, and

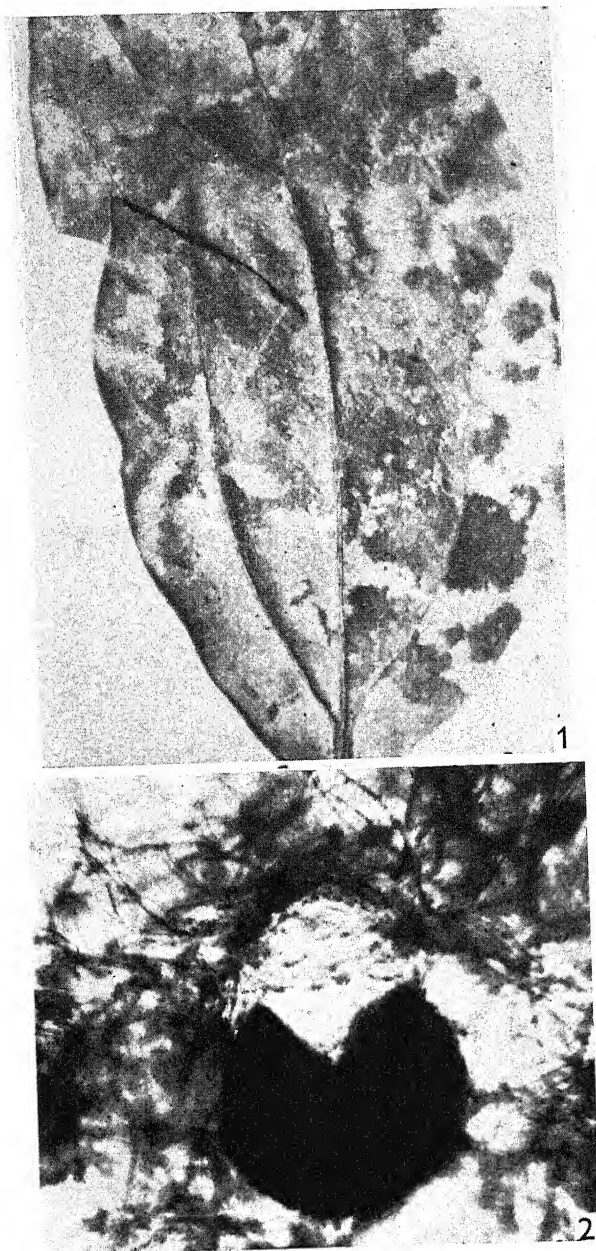


Fig. 1. Photograph of the leaf of *Neolitsea zeylanica*. $\times \frac{3}{4}$ nat. size.

Fig. 2. Photomicrograph showing the dehiscence of the perithecium. \times about 400.

Perisporiaceae of Clements & Shear (1931), who group all the three families under Perisporiales. In Eurotiaceae most of the members are saprophytic, the asci being formed irregularly or in corymboid clusters. In both Erysiphaceae and Perisporiaceae, on the other hand, the asci are basal in umbellate clusters, a character found in the present genus also. The genus *Astomella* might therefore be placed either under Erysiphaceae or Perisporiaceae. In this connexion it might be pointed out that *Lanomyces* Gaumm., which has coloured mycelium unlike most of the other genera of Erysiphaceae, is placed by Gaumann between Erysiphaceae and Perisporiaceae and under Erysiphaceae by Clements & Shear. The genus *Astomella* might also be placed along with *Lanomyces* as an aberrant genus under Erysiphaceae, having perithecia with many asci and once septate spores.

The coloured mycelium and the bright reddish brown perithecia recall the characters of the Nectriaceae. However, the type of dehiscence of the perithecia is quite unique and differs from the methods of dehiscence so far known in the related groups.

In conclusion, the writer wishes to acknowledge his deep sense of gratitude to Mr C. G. Hansford, Kampala, Uganda, for carrying out most of the preliminary work on the fungus and for pointing out to the writer the systematic position of the genus. Grateful thanks are due to Dr S. P. Wiltshire and Mr E. W. Mason of the Imperial Mycological Institute, Kew, England, for going through the manuscript and for giving literature about *Cryptothecium*. Rev. Dr H. Santapau, Professor of Botany, St Xavier's College, Bombay, very kindly prepared the Latin diagnosis of the genus and species.

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A NOTE ON THE ASSIMILATION OF CARBON DIOXIDE BY APPLE FRUITS AFTER GATHERING

BY F. KIDD AND C. WEST

(With 1 figure in the text)

In view of the fact that apples contain chlorophyll, one would expect carbon-assimilation to occur in fruits exposed to light. We were interested to know how much assimilation, if any, occurs in apples exposed to light both on the tree and after gathering since if the quantity of carbon directly assimilated were large, it would have to be taken into account in the study of the chemical changes which take place during the growth and senescence

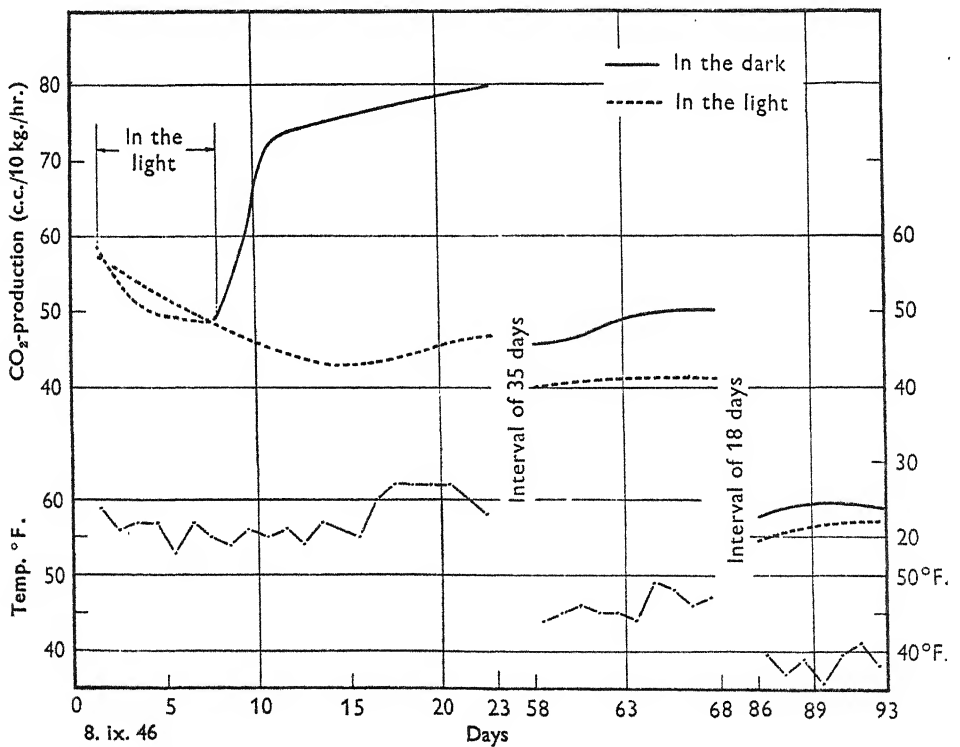


Fig. 1. CO₂-production of Bramley's Seedling apples in the dark (solid line) and in the light (dotted line), after detachment from the tree.

of the fruit. No information on this point could be found in the literature. Two experiments were therefore carried out; one with Bramley's Seedling apples gathered on 25 June (av. fresh weight 40 g.), and another with Bramley's gathered on 8 September (av. fresh weight 115 g.). The experiments were carried out in the orchard without temperature control. Both the darkened fruit and the fruit exposed to daylight were shielded from direct sunlight and were at sensibly the same temperature. The first

experiment extended over a period of 10 days after gathering. The second was continued for 3 months, during which time the normal climacteric rise in respiratory activity took place. The CO_2 -production during successive 24 hr. periods was measured.

In both experiments CO_2 -production was considerably less in the light than in the dark (Fig. 1). The excess CO_2 -production in the dark was as follows:

First experiment, 40 g. fruits (25 June–5 July), 48 mg. (24 c.c.) $\text{CO}_2/\text{M}^2/\text{hr.}$ (including hours of darkness).

Second experiment, 115 g. fruits (17–29 September), 64 mg. (32 c.c.) $\text{CO}_2/\text{M}^2/\text{hr.}$ (including hours of darkness).

Schneider & Childers (1941) measured the apparent assimilation in July of leaves of apple trees grown in 5-gallon glazed stone crocks in the open, exposed freely to the weather conditions of Central Ohio, U.S.A. Values (mg. $\text{CO}_2/\text{M}^2/\text{hr.}$) varied from 500 to 4000, and over 16 days averaged about 1500.

It therefore seems probable that the photosynthetic activity of the fruit per unit surface is a tenth or less of that of the leaf and that the contribution to the increase in dry weight of the fruit during its growth made by photosynthesis in the fruit itself is small.

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NOTE ON THE DIURNAL FLUCTUATIONS IN WATER CONTENT OF FLOATING LEAF DISKS

By P. E. WEATHERLEY

(With 2 figures in the text)

Recently attempts have been made in Uganda to follow variations in the water content of leaves of cotton plants growing in the field. The technique used involved floating punched leaf disks on water for periods of about 24 hr.

Phillis & Mason (1945) working on cotton in Trinidad have reported marked diurnal variations in the water content of floating leaf disks, and have suggested that since it is unlikely that floating disks could suffer a water deficit in the usual sense, light might be a causal factor. The present writer was unable to detect any diurnal variations in the water content of floating disks such as found by Phillis & Mason. Nevertheless, the question needed further investigation, for the existence of such a complication is important in any floating-disk technique designed to give information about water deficits.

A comparison of the techniques used in Trinidad (Mason & Phillis, 1942) and Uganda gave a clue as to the cause of the diurnal fluctuations found by Phillis & Mason. In Uganda a punch of very nearly 1 cm. diameter was used and the disks were floated with adaxial surfaces uppermost, in Trinidad a punch of about 1.9 cm. diameter ($\frac{3}{4}$ in.) was used and the disks floated with abaxial surfaces uppermost. The two methods of floating and two disk sizes were compared.

Two sets of 1 cm. diameter disks were punched: one set was floated with adaxial, and the other with abaxial, surfaces uppermost. One set of 1.9 cm. disks was floated with abaxial surfaces uppermost. From time to time the disks were removed, surface dried with filter-paper and fresh weights found. Before removal all disks were totally submerged for a few moments, before drying. There was evidence that fresh weight changes largely reflected changes in water content under these conditions. Fresh weights expressed as percentages of initial values are shown in Fig. 1. It will be seen that there was no detectable difference between the two sets of 1 cm. disks, neither of which showed any signs of diurnal fluctuations. On the other hand, slight but definite diurnal fluctuations occurred in the 1.9 cm. disks.

This experiment indicated that the occurrence of diurnal fluctuations in water content of floating disks was related to the diameter of the disks. To explain this the simplest hypothesis seemed to be that absorption took place only at the cut edges of the disks: thus the ratio between transpiration (area of disks) and absorption (circumference of disks) was defined by the size of the disks. In the case of the 1 cm. disks the ratio of absorbing edge to transpiring surface was such that transpirational loss could always be equalled by absorption. On the other hand, in the case of the 1.9 cm. disks with a greater transpiring surface per unit absorbing edge, the water content fell a little in the heat of the day.

If this hypothesis were correct, it should be possible to eliminate these diurnal fluctuations in water content by maintaining an atmosphere of high humidity over the disks. This was attempted in a second experiment which was of the same type as the first, fresh weights being followed in floating disks. Six sets of 1.9 cm. diameter disks were floated

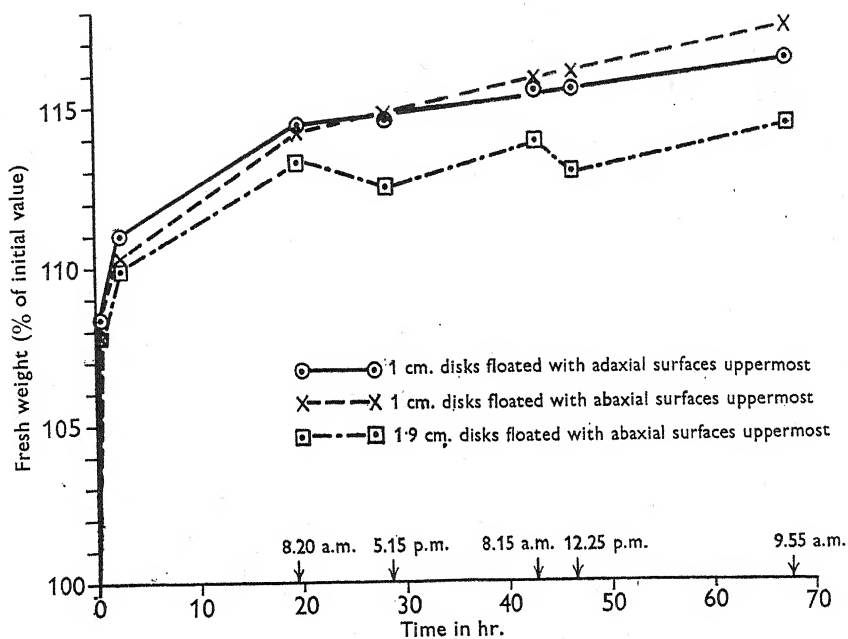


Fig. 1. Curves showing effect of disk size and method of floating on water content of floating disks

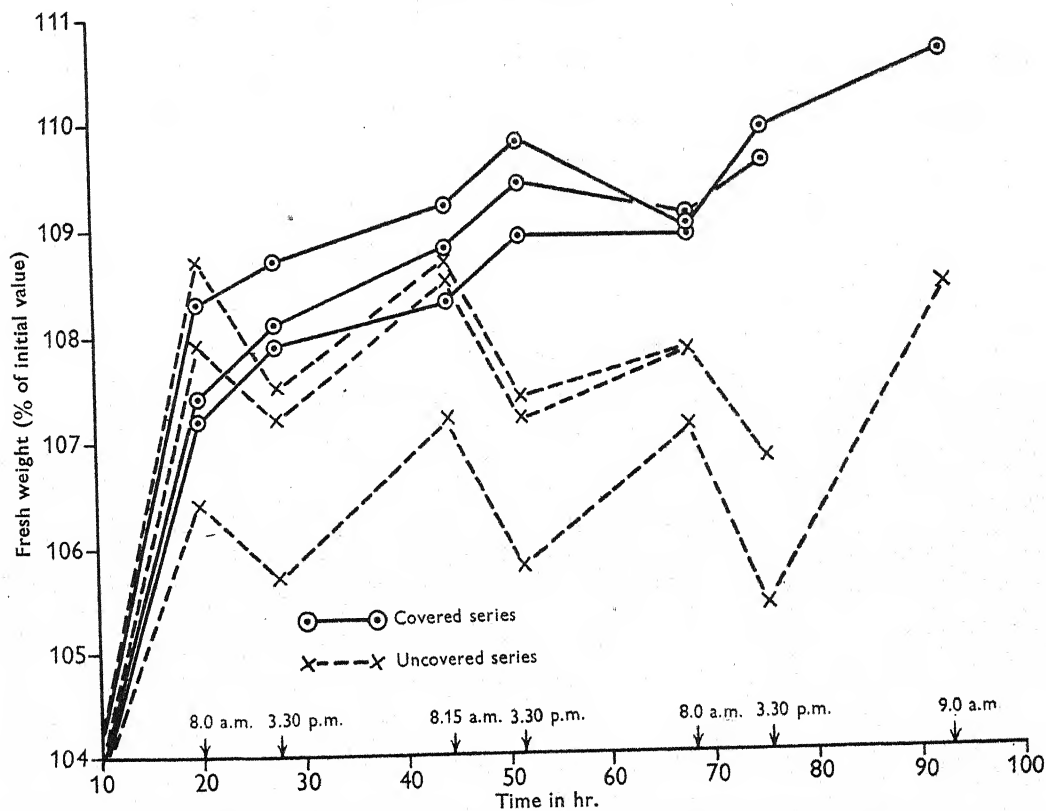


Fig. 2. Curves showing the effect of atmospheric humidity on diurnal variations in water content of floating disks.

with abaxial surfaces uppermost, in six large petri dishes placed in bright diffuse light near a window. After all the disks had floated for 20 hr., three of the petri dishes were chosen at random and covered by glass lids: these constituted the covered series. The remaining three dishes were left open and constituted the uncovered series. At night all the dishes of both series were covered with glass lids, but these were not closely fitted as in the case of the covered series during the day, the lids were raised a little to allow free passage of air and so prevent excessive condensation, resulting from the drop in temperature at night. Excessive condensation might have occurred on the surface of the disks preventing gaseous exchange, or even submerging them. No such condensation took place. Light conditions were very uniform over both series. At the times of the last three readings, one set from both series was removed, and water contents determined by oven drying. This was done to confirm that the fluctuations in fresh weight really reflected changes in water content.

Fresh weights expressed as percentages of initial values are plotted in Fig. 2. It will be seen that the uncovered series showed well-marked diurnal fluctuations. The covered series showed no such fluctuations, indeed they showed slight diurnal variations in the opposite direction, to the uncovered series. The probable reason for this adds force to the hypothesis that these diurnal variations were due simply to fluctuations in atmospheric humidity over the disks. The covered series were more closely covered during the day than during the night, so that in fact a greater humidity was maintained over them during the day than during the night. This was reflected in a slightly less fresh weight in the morning, and a slightly greater fresh weight in the afternoon, than would be expected from the general slope of the graphs.

The water contents supported the fresh weight readings, indicating marked diurnal change in the uncovered series and relatively little change in the covered series.

	Weights in g. per sample		
	8.0 a.m.	3.30 p.m.	9.0 a.m.
Covered	1.20	1.21	1.20
Uncovered	1.20	1.12	1.19

The errors of sampling were such that these figures can be taken to support the presence of a diurnal fluctuation in the uncovered series and its absence in the covered series, but not to indicate the magnitude of the fluctuation.

CONCLUSIONS

1. Uptake of water by floating disks occurs along the cut edge and not over the whole surface in contact with the water.
2. The diurnal fluctuations in water content of floating disks can be explained simply in terms of transpiration and absorption.

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- STUBBE, Prof. Dr. H., Gattersleben, Bez. Magdeburg.
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 ZIEGENSPECK, Dr. habil. Hermann, Apotheker, (13a) Kötzing (Bayern), Adlerapotheke.
 ZIMMER, Walther, Studienrat, (10) Kamenz i. Sa., Arendtstr. 29.
 ZIMMERMANN, Prof. Dr. W., Tübingen, Wilhelmstr. 5.
 ZYCHA, Doz. Dr. H., Hann. Münden, Friedrichstr. 4.

REVIEWS

Les Associations Végétales de la Vallée Moyenne du Niger. By G. ROBERTY. 9 × 6½ in. Pp. 168, with 2 text-figures and 1 folding map in colours. *Veröff. d. Geobot. Inst. Rübel in Zürich*, 22. Heft. Bern: Hans Huber, 1946. Price Swiss Fr. 12.

Continental phytogeographers seem obsessed with the analogy—surely a very superficial and not very helpful analogy—between the taxonomic hierarchy of species, genus, family, order, etc., and the phytosociological hierarchy of societies, associations and formations (or whatever units one prefers to use).

Dr Roberty, grappling with the multitudinous plant communities of tropical Africa, feels that the task of the plant geographer would be lightened if each community were given a brief and precise description similar to the taxonomic diagnosis of a genus or species. Originally he intended to write these descriptions in Latin, but owing to the intervention of Dr Lüdi (for which most readers will be grateful), he retranslated them into French, retaining 'le style linnéen, presque un style télégraphique, sans verbes et sans incidentes, dont le défaut d'éloquence nous semble largement compensé par la clarté'. The descriptions are indeed clear, but it may be doubted whether the author has succeeded in his object which he says is to describe the communities so that a naturalist dropped from a parachute would at once recognize the community in which he found himself. The technique of describing plant communities, like that of describing species, still has much room for improvement and brevity is often a virtue, but in the reviewer's opinion more attention to the physiognomy of the constituent species and to features of structure which can be expressed quantitatively or represented in a profile diagram would be more likely to lead to progress than aping the methods of the taxonomist.

It is not only in his 'Linnean' descriptions that Dr Roberty is unconventional, but also in his units and their nomenclature. Abandoning the accepted phytosociological units, he adopts a new hierarchy of his own, the *paysage* which is approximately the equivalent of the association (and the 'geographical equivalent of the species'), the *secteur* and the *domaine*, the last more or less synonymous with the zone or region of other phytogeographers (thus the Saharan, Sahelian, Sudanian and Guinea zones of West Africa are *domaines*). These units, it seems, were proposed by Dr Roberty in an earlier paper (not available to the reviewer) and their advantages are not clearly explained in the present publication.

The difficulty of naming tropical plant communities in which so often several or even a large number of species are co-dominant is generally admitted and has not yet been satisfactorily overcome. Is it, however, a step forward to renounce the usual method of constructing names ending in *-etum* and in their place to concoct 'des noms entièrement nouveaux, barbares peut-être, mais, nous l'espérons du moins, précis et non confus'? Not confused, we may freely admit, but a burden to the unfortunate reader's memory already strained by the names of the dominant species! Some of Dr Roberty's new names are personal; thus one of his *secteurs* is called Chudealium after the French naturalist and explorer Chudeau, another Augusteum after M. Auguste Chevalier. Well deserved as are these tributes to distinguished predecessors, one can foresee that if Dr Roberty's method of nomenclature becomes popular not only a Braun-Blanqueteum lies in store for us, but British ecologists might wish to stake out a claim for a Tansleyeum or a Wattialium.

The region described is part of the Niger valley lying between 12° 30' and 15° 30' N. and between 4° and 8° W., part of it included in the Sahelian Zone and part in the Sudanian Zone; there are also 'irradiations' of the Guinea Zone (gallery forests, etc.). The systematic description of the very numerous communities occupies the greater part of the book. This description is followed by a dichotomous key to the communities (modelled, we are told, on the form of taxonomic key used in the *Conservatoire botanique de Genève*) and by a *synthèse théorique* in which the author's views on the dynamic relationships of his communities are somewhat obscurely presented. The book closes with a regional account of the distribution of the communities and a gaily coloured vegetation map of a portion of the area.

P. W. RICHARDS

Botany, Principles and Problems. By EDMUND W. SINNOTT. 9 × 6 in. Pp. 726; 403 figs. and frontispiece. New York and London: McGraw-Hill Book Company, Inc. 4th edition. 1946. Price 22s. 6d.

This is a delightful and stimulating book to use; the approach to and treatment of the various branches of botany are always original and full of vigour, and the science as a whole is presented as a live and growing one.

The fourth edition is considerably larger than the third; new chapters on 'Plant distribution' and 'Botany and the future' have been added; much more stress has been laid on the economic importance of plants and their various parts; sections have been added in various chapters to include modern views and results, including cell physiology, osmotic relations and absorption of ions, the energy problem, the part played by the essential elements, vitamins and viruses. The chapters dealing with heredity and evolution and the vascular plants are extended, many more types being included in the last mentioned, and the chapter on Bryophyta has been completely rewritten by Prof. Hempstead Castle.

Inevitably there are defects in a book which attempts to cover so much ground. To English eyes the treatment appears somewhat unbalanced with too much weight given to development, morphogenesis, heredity, variation and evolution and too little to metabolism in general and to the ascent and loss of water and to ecology. The account of nuclear division (mitosis) ignores the work of Darlington and others in this country and in the U.S.A. but refers to spindle-fibres and formation of the cell-plate from them. The ascent of water in tall trees is dismissed in one very brief section, with only two or three sentences referring to the cohesion theory of Dixon and Joly and a passing reference to the influence of transpiration on the movement of water. The translocation of dissolved organic substances is also very inadequately discussed, though admittedly this is much more difficult to deal with from an elementary point of view. In the section on metabolism there are several misstatements, such as the sentence on pp. 189 and 201 implying that respiration involves the breakdown of protoplasm; and that on p. 206 where respiration and photosynthesis are declared to be 'the precise reverse or reciprocal' of one another. The definition of oxidases on p. 205 is also very unorthodox. Nothing is said about the role of phosphates in respiration and fermentation and more might have been said about the role of ascorbic acid and co-carboxylase (thiamin diphosphate, not thiamin, as stated on p. 211) in plant metabolism, especially when so much space is devoted to the relations of vitamins to plants.

The book is freely and very well illustrated, the weakest point in this respect being the illustrations dealing with flowers. These are few and poor.

On the whole, the book may be strongly recommended. It is, perhaps, not suitable as a text-book to parallel a course in this country, but certainly it should be in all botanical libraries and should be read by all students to broaden their outlook and stimulate their interest. G. M. JAMES

A Textbook of Systematic Botany. By DEANE B. SWINGLE. 8½ × 5½ in. Pp. 343, 106 text-figures, frontispiece. New York and London: McGraw-Hill Book Company, Inc. 3rd edition. 1946. Price 17s. 6d.

Presumably there is a demand for this book since a third edition has been prepared. It has some useful features but unfortunately is marred by an uncritical outlook and by gross mistakes of fact. The title is misleading. At most it can claim to be a 'Text-book of Families of Seed-bearing Plants'.

The main objection to the theory underlying the teaching embodied in this work is the total failure to define adequately what is meant by 'artificial' and 'natural' in plant classification. It is again and again, stated, in varied words, that classification 'must show actual phylogenetic relationships'. Since, however, these, with very few exceptions in the Angiospermae, are unknown and can only be assumed from indirect evidence as more or less possibly this or that it seems absurd to pretend that plant classification is, at present, founded on anything more than resemblances and differences and may therefore help in elucidating phylogeny but cannot be based on it. The greatest gap in knowledge of the flowering plants is their early history. Till relevant fossil data become available their origin, and consequently any certainty as to which are the most primitive of their families, is a matter too hypothetical to be of much use in the theory and practice of their

classification. Actually so-called phylogenetic classifications, as that of Bessey which is used in this book, are essentially 'logical' not 'phylogenetic'. At most, the use of what are here termed 'morphological indicators of phylogeny', may give suggestions favouring one or another of several possible positions in the linear sequence of groups which is the final form assumed by a practical classification. It is, of course, highly probable that a logical classification, founded on maximum correlation of as many characters as possible, most often coincides with the phylogeny of the groups classified, as nearly as phylogeny can be expressed in classification. To this degree, 'logical', 'general', 'phylogenetic', and 'natural' classifications may well be nearly synonymous, in their ideals, and contrast with 'artificial' classifications which are based on a few selected characters.

One's respect for phylogenetic hypothesis, as set forth in the present work, is not increased on comparing such statements as the following: 'It is pretty generally agreed that flowers have been evolved from the strobili of pteridophytes' (p. 296) and 'It is generally conceded that flowers evolved from the strobili of gymnosperms' (p. 297).

There is much of interest and value in the introductory chapters concerning the making of keys, the preparation of herbaria, and the terminology of systematic (spermatophytic) botany. In the later chapters, the inclusion of an account of nomenclature is to be commended but this should have been more carefully prepared. For example, the fifth international botanical congress was not held in London in 1930, but in Cambridge, England.

The central chapters deal with the families of Dicotyledons and Monocotyledons. Outline accounts are given of family characters and economic uses of species in the family. Naturally most of the examples are North American but the presentation has little to distinguish it from other text-book treatments of 'families'. Some of the figures are exceedingly poor and some (as Figs. 85 and 86) even grossly inaccurate. The work, as a whole, cannot be recommended to British students.

W. B. TURRILL

Botany by Observation: A Text-Book for Australian Schools. By GLADYS CAREY.

8½ × 5½ in. Pp. 356, 205 plates and figures in the text. Sydney and London: Angus and Robertson. 1946. Price 12s. 6d.

This book, written by a member of the staff of the Department of Botany, the University of Sydney, who herself has 'taught School', provides an introduction to the subject based upon the requirements of the Leaving Certificate in New South Wales. Written primarily for the needs of children working in Sydney the book should nevertheless be of considerable help to both pupils and teachers in other parts of the Commonwealth. Obviously the book will have less utility outside Australia though certain features are valuable, notably the account of floral mechanisms in unfamiliar types and the short ecological description of plant life in the Sydney district.

Probably nobody who has not actually met them in the hard school of experience can appreciate the difficulties which confront a teacher of botany in Australia. These difficulties are great enough at the University level, though there the relative maturity of the student allows him to make some mental adjustments between what he reads in European and American text books and what he observes in the plants growing around him. For the school teacher things are harder. Clearly the school child cannot be expected to read widely as an undergraduate and the need of some one text book which the pupil can study for himself is obvious. The need was acute enough even 40 or 50 years ago when, at an elementary grade, angiosperm morphology still stood first in elementary courses. Even then, as von Mueller writes in the preface to his *Botanic Teachings* (1877): 'the only method... consists in arousing the interest of the young scholars in the native plants of their own locality.' But the turgid style and floristic approach of the old Baron have long ceased to have any appeal to, or even much educational value in, modern schools. It is all very well for the various Australian school examination syllabuses to lay down that the approach to botanical study must be by experiment and field work. From whence, apart from the dictated and carefully handed-down 'notes' of the teacher himself, is the information and guidance to come? Modern British or American text books are rather unworkable things in the hands of the Australian school child. It is even more startling to discover that the better the book, the more it is permeated by a knowledge of the countryside, the more fully it refers to the biology of northern hemisphere plants, the more unhelpful it becomes. Nor can such a book be satisfactorily rewritten as an Australian edition. The changes involved are too radical, the whole background of experience of the children is too

different. It is not only that in the southern hemisphere the seasons are reversed and that aestivation is as important for some plants as hibernation to others. That is obvious. But in Australia there are no meadows or fields with their occasional ponds surrounded by rushes and with a marshy stream meandering through them with distant woods beyond. There are 'paddocks' which may contain water troughs or 'dams', divided by wire fences. Trees, apart from those used in street planting or grown in gardens, are either plantations of exotic conifers or occur in the 'bush'. Of course there are vast cultivated areas, but the school child in Sydney must travel 100 miles or more to see a wheat-growing district. The deciduous tree he knows from planes or fruit trees, but oak, beech and birch are unfamiliar. He knows the Jaracanda and silky-oak. He knows their buds and that they are very different from that of the horse chestnut which even in Miss Carey's book remains as the typical scaly bud. Of course he has access to a far greater range of garden plants than his British counterpart but almost all of them are foreign. The flowers and fruits that he sees in the bush, with their harsh evergreen leaves that he is too frequently misleadingly taught to call xerophytes, are referred to in no text book available to him.

Why, it may be asked, was no suitable book written before? There are many reasons, such as lack of time on the part of the few qualified persons. One is economic, for the school population requiring such an elementary botanical book, though increasing, is small. Botany is still in the main a girls' school subject in Australia in spite of the fact that it is the scientific basis of agriculture and required by the very considerable number of medical or pharmaceutical students. A second reason is that of lack of essential information on the part of those otherwise qualified to write. Only comparatively recently has field work with a biological and ecological outlook been undertaken in the Commonwealth. Even now the fund of information is woefully small compared with the wealth of local knowledge which is open to the author in Britain. Miss Carey has made an altogether praiseworthy effort to tackle the problem. Her title indicates the method of approach. Her book will be little use for cramming because she assumes that it will be studied together with the specimens. The descriptions of experiments—and they are many and interesting—rarely give results. These are to be found out by the pupil himself. In using the book the teacher is helped by notes at the end of each chapter and at the end of the book.

The method with which the subject is introduced is perhaps a little unusual nowadays. It starts off with a very solid dose of morphology; but logically from this beginning it passes to a brief consideration of soil, root systems, transpiration, nutrition and irritability. After an introductory study of the flower, a number of species are considered as illustrating types of floral mechanism, not, as Prof. Ashby says in his introduction, 'as examples of the emaciated taxonomy of the schoolroom'. The book concludes with a slight but interesting account of the ecology of the Sydney district; an account the writing of which has only been made possible by the research work of several of Miss Carey's colleagues as well as her own.

It would be unreasonable to expect that the first edition of a book of this kind should be entirely without mistakes. Typographical errors are not apparent, but there are some slips that should be corrected in the second edition which will surely be needed. The fruit of Jaracanda is a bicarpellary loculicidal capsule, and not a legume (p. 248). The operculum of a eucalypt bud is probably a modified corolla—not calyx (p. 243)—or how are the teeth found in the subsection Eudesmieae to be explained? There is an extraordinary statement on p. 341 about the capitalization of Linnean specific names. It would save much unnecessary trouble were botanists of the Dominions to follow the bold lead of the editors of the Ecological Flora in the mother country and abolish all capitals for specific epithets.

The book is freely illustrated with both line drawings and half-tones. These really form a series of plates but they are not separately numbered. Some of the photographs used here are derived from the work of Drs Pidgeon and Fraser on the local ecology. Most of the line drawings are satisfactory, some attain to the standard of excellent; but others are more diagrammatic and a few might well be replaced. The pollen tubes on p. 211 are truly remarkable and it is unfortunate that the pea-pod on p. 213 should have been drawn open along the dorsal suture. But of the final conclusion there can be no doubt. Author and publishers are to be congratulated. The book cannot but have an important beneficial influence on the development of botany as a school subject in Australia.

T. G. B. OSBORN

Leguminous Forage Plants. By D. H. ROBINSON. Demy 8vo viii + 119 pages ($8\frac{1}{2} \times 5\frac{1}{2}$ in.) 35 text-figures as from drawings. Edward Arnold and Co., London. Second edition, 1947. Price 7s. 6d.

The second edition of this book differs only from the first in having certain sections brought up to date, and a new illustration provided for one of the figures. The book has already proved its worth for agricultural students in providing an elementary account of the leguminous forage plants, including a description of diagnostic characters from seed to mature plant, history, uses, strains, seed production and chemical composition. There is no other agricultural text book that covers the same field, and the treatment is very suitable for agricultural colleges and institutes.

G. D. H. BELL

Handbook of the Trees of the Northern States and Canada, east of the Rocky Mountains. By ROMEYN BECK HOUGH. $9\frac{3}{4} \times 6\frac{1}{2}$ in., pp. 476, with 479 photographic illustrations and numerous maps. New York: Macmillan Co. 1947. Price 28s.

In the author's words this handbook is defined as dealing with 'the native and naturalised trees of the region of North America lying north of the northern boundaries of North Carolina, Tennessee, Arkansas and Oklahoma and east of the Rocky Mountains, and extending southward in the Appalachian region to northern Alabama and Georgia'.

It has been compiled for the use alike of professional botanists, foresters, and interested students less technically concerned with tree identification. The plan consistently followed has been to allot two facing pages of smooth-faced paper to each of 200 odd species of native and introduced trees, and upon this space to provide suitable photographs and description. In all instances there is a photograph of the mature (but not ancient) tree bole, and a full page photograph of leaves, flowers, fruit, seeds, leafless twigs etc., taken upon a background of 1 inch squares. In most instances a simple but very useful distribution map is included, and often a photograph of a low-power magnification of the wood in cross-section.

The generalized and popular description deals with the habit and natural history of the tree, and the outline of the values of its timber. A short technical botanical account allows an accurate identification to be achieved. The last 52 pages of the book are taken up with a good index, a comprehensive glossary of botanical terms, and a synopsis of the families and genera represented in the book, together with keys to the species identification.

The value of this handbook to the botanist not living in North America will lie partly in the fact that it describes the native occurrence of woody species now introduced into many other parts of the world, but probably to a greater extent in providing a general fund of knowledge of the tree species of that remarkable area of the South Eastern U.S.A., in which the ancient Tertiary forests in modified form still persist. There is no claim that this work is a comprehensive flora, or that it displaces any existing flora; critical separation of species is not an avowed aim and we find for instance the plate of *Crataegus monogyna* Jacq., labelled under the wider Linnean name *C. Oxyacantha*.

It is a great pity that the production standard of the book should not altogether have realised its full potentialities. The tree-trunk photographs are flat in tone, and those of twigs and leaves lack quality so badly that important details of bud-scales or flower- or fruit-structure cannot be made out. In fact several scales of enlargement are necessary to display all features of the organs brought into the pictures, and it would be well to try to avoid the stiff and withered look which is so familiar in the dried herbarium specimen, and so unfamiliar in the fresh material in the hand or on the tree. Possibly further editions may see these faults remedied.

H. GODWIN

A Botanical Bibliography of the Islands of the Pacific. By ELMER D. MERRILL; and a Subject Index to the same, by E. H. WALKER. $9\frac{3}{4} \times 6$ in., pp. 404. Contributions from the United States National Herbarium, 30, 1. Smithsonian Inst., Washington, D.C. 1947. Price \$1.00.

The spread of intensive warfare to the Pacific world strikingly showed up scientific ignorance of its innumerable islands, and emphasized the need for coordination of the knowledge we have, as well as for further investigation. Dr Merrill, Director of the Arnold Arboretum, has now produced

a botanical bibliography of the islands of the Pacific. It includes 3850 author references from the date 1773 onwards, and deals with an area between latitudes 30 N. and 30 S. (excluding the Bonin Islands), and from Hawaii and Juan Fernández in the east to the western limits of the Marianas, Caroline and Palau Islands.

Monographic works dealing with the plant species of the Pacific, general botanical works, phytogeographic and ecological accounts, works on travel, on plant pathology, forestry, horticulture, and some phases of agriculture are included, and algae, fungi, lichens, bryophyta, pteridophyta and spermatophyta all are brought in. Papers on plant physiology, genetics, cytology and morphology have however been excluded.

The value of the work has been much enhanced by a detailed subject index and short geographical index, which have been compiled by E. H. Walker.

H. GODWIN

Advances in Genetics. Vol. 1. Edited by M. DEMEREC. Pp. xvi + 458. Academic Press Inc., New York 10, U.S.A. Price \$7.50.

This is the first of a series of volumes of review articles and critical summaries of outstanding problems in genetics. The Editorial Board includes many eminent American geneticists, who have invited specialists in various fields of genetical research to prepare reviews of existing knowledge and current ideas in their own particular fields. Volume 1 comprises ten such reviews, ranging in content from academic subjects such as the genetics of *Paramecium*, to matters of interest mainly in the field of applied science—for example the genetics of cattle. The articles maintain a high standard throughout. They are authoritatively written and well documented with references. In a number of cases, new ideas are expressed which are stimulating to the reader though perhaps not always readily acceptable.

The first article is an account of 'Cytogenetics and Breeding of Forage Crops' by S. S. Atwood, with a bibliography comprising 350 references. It would have been helpful to the English reader if the Latin names of the genera had been included in the titles of the various sections, since several of the popular American names are not in common use in Britain. For each species or group of related species an account is given of cytological and genetical investigations, and of breeding experiments designed to improve the stock from the commercial point of view. The article includes a summary of the breeding methods that have been applied to forage crops.

The second article, entitled 'Cytogenetics and Speciation in *Crepis*', is by E. B. Babcock. Few natural groups of flowering plants have received cytological and hybridization studies so detailed and comprehensive as have been applied to this group of nearly 200 closely related species of the genus *Crepis*. Some 113 species have been studied cytologically and, except for 15 polyploid species, have been found to have haploid chromosome numbers ranging from 3 to 7. Evidence is presented to show that the primary processes of species formation in *Crepis* have been interchanges between segments of non-homologous chromosomes and gene mutation. Factors of lesser importance have been interspecific hybridization, polyploidy and apomixis, all of which characterize in particular the origin of the American species of *Crepis*, which are chiefly allopolyploids with the haploid chromosome number of 11. There can be little doubt that the species with 3, 4, 5 and 6 haploid chromosome numbers represent an evolutionary series, but whether the primitive species had 6 chromosomes, as the author concludes, or a smaller number, would appear uncertain on the evidence presented. The article would benefit by an account of the morphological characteristics of the *Crepis* species which are considered to have evolutionary significance, and the reasons why they are to be regarded as primitive or as advanced features.

The third review is by M. Gordon on 'Speciation in Fishes', with the sub-title 'Distribution in Time and Space of Seven Dominant Multiple Alleles in *Platyfocilus maculatus*'. This species of platyfish inhabits four different river systems which enter the Gulf of Mexico at intervals of 50 to 100 miles along its southern shore. The various tail patterns of this fish found in nature have been shown by breeding experiments to be controlled by seven dominant allelomorphs at one locus, with a single universal recessive gene. It has been shown that the platyfish population of each of the four river systems has its own characteristic frequency of the genes for tail patterns. The analysis shows how geographical isolation can lead to differences in the gene frequencies or gene content of different parts of the population of a species, and it suggests how divergences might accumulate until ultimately several species would exist where formerly there was but one. The author makes clear that the term speciation is used to include the lowest level of genetic differentiation, as

Rhacomitrium lanuginosum, however, appears among the elect, with suitably apologetic text. The relation to habitat, as indicated for some of the species (*Plagiothecium undulatum*, *Polytrichum commune*, *Mnium hornum* compared with two of the subsequent species), is at variance with experience further south. The omission of *Brachythecium rutabulum*, possibly the most widely common of all our woodland mosses, with a wide soil tolerance, can be justified by the booklet's declared purpose, which is, indeed, highly laudable. This is to bring to the attention of foresters the means of recognizing certain of the larger common mosses of woodland, with a view to their use as indicators of soil conditions.

The qualifications of a species for inclusion in a work of this kind would seem to be (1) easy recognition in the field, and (2a) known value as an indicator of conditions not otherwise obvious or (2b) possible indicator value which might be brought to light by foresters' observations, duly reported and correlated. Easy recognition has clearly been considered. A more rigid application of the second principle, with a fairly full statement, for each moss chosen, of its claim to inclusion under either (2a) or (2b), might produce some advantageous changes of species-content and enhance the eventual return in information. Wet, heathy or peaty conditions, for example, must be evident to an observant woodsman, more often than not, without conscious recognition of *Sphagna*. On the other hand observation of a moss such as *Porotrichum alopecurum* (not included), which is unmistakable and common though not ubiquitous, might well prove useful.

The text is brief, relevant and spontaneous—sometimes excessively so, as where the 'swollen obtuse stems' (shoots) of *Brachythecium purum* are contrasted with the red stem of *Hypnum schreberi*. The illustrations, surviving a shaky protonema in Fig. 2, contribute a series of handsome and lifelike portraits of moss turf, at or near natural size (although this is not stated). Companion photographs of single shoots are much less successful. For instance that of *Sphagnum cymbifolium* 'with broadly ovate leaves' (which are virtually invisible) shows far less detail than its companion turf. With its quota of the luxurious amount of empty white space allowed throughout the book, it accounts for the unnecessary use of a whole page. Such ample resources of glazed paper, used for print as well as photographs, must be the envy of hard-pressed editors and publishers in less official circles. They seem at least to merit a finer half-tone screen than has been used and, for that matter, a form of binding less prone to tear away from the sheets.

Semi-popular booklets of this kind have great potential value, and the present one by no means lacks actual value. The circulation might be large, the intentions are admirable, and it is stated to be the first of a series. Such circumstances warrant every care in content and presentation.

J. F. HOPE-SIMPSON

The Evolution of Gossypium and the Differentiation of the Cultivated Cottons. By J. B. HUTCHINSON, R. A. SILOW and S. G. STEPHENS. 8½ × 5¼ in., 160 pp., 10 figs. Oxford University Press. 1947. Price 15s.

This important book should have a much wider circle of readers than one composed solely of botanists interested in the cottons. It is well written, summarizes a great deal of modern genetical and cytological research in *Gossypium*, and relates such research to many of the problems connected with the origin and development of the genus and its constituent units. There is no attempt to force the evidence to explain the evolution of all groups of organisms but it is self-evident that the experimental and observational facts here recorded for *Gossypium*, and the reasoned explanations suggested as their theoretical background, will have to be taken into account by everyone attempting to synthesize the results and methods of the evolution of plants.

Twenty species of *Gossypium* are accepted, some with varieties, the latter being what would be called subspecies on some standards. The problems of speciation are the concern of much of the theoretical discussion. It is pointed out that the genus has a great advantage for evolutionary studies in that 'it embraces within the limits of what is certainly a monophyletic group, species of extremely different biological status and evolutionary history'. In particular, there are important differences between the wild and cultivated species. The former show large morphological distinctions that are matched by crossing barriers or cytological differentiation. In the cultivated cottons there is a 'vast range of variability which has given rise to taxonomic confusion, the morphological differences between true species are comparatively small, and crossing barriers and cytological differentiation are confined to those consequent on polyploidy'. The linted cottons

achieved their success from the evolution of two new characters, convoluted lint hairs and the annual habit. Such mutations may have arisen many times before civilized man recognized their value and commenced a long process of selection of very different kind from that occurring in the wild. Cultivation and weeding reduces the pressure of selection in the early stages but leads later to the intensification of intra-specific competition. Characters essential for successful survival in natural vegetation became progressively lost in the commercial cottons. On the other hand, man has acted as an agent of intensive selection, particularly for the annual habit.

Cotton was first used in the Indus valley but the progenitors of the early economic cottons must have been introduced from southern Arabia or north-eastern Africa. The basic chromosome number in the genus is $n=13$, and all species have $n=13$ or $n=26$. The polyploids include the cultivated New World species and the wild *G. tomentosum* from Hawaii. The cultivated tetraploids have been shown to be allopolyploids with a set of 13 chromosomes, homologous with the genome of the cultivated Old World species, and a set of 13 homologous with that of the wild American species. It is postulated that the Old World diploid parent was carried by man across the Pacific. This hypothesis agrees with many known facts and is in accord with the cytogenetic evidence for a relatively recent origin of allopolyploidy in the American cottons.

The taxonomic, phytogeographical, and cytogenetical evidence suggests a very different explanation for the development of the wild species. 'If continental drift may be accepted, then, the differentiation of a primitive Angiospermous genus into the three major continental groups of species of *Gossypium* may well have taken place following the break up of the great Jurassic arid area into continental arid zones in the Cretaceous period.' Objections may be raised to this view which requires fuller consideration than it has yet been given.

The significance of polyploidy is discussed rather fully towards the end of the book and many matters of wide general importance emerge. It is shown that the possibilities of variation in a polyploid are no less than in a diploid, and that much of the variability arising by mutation will be subject to selection from the beginning. There is a general tendency towards a restoration of the diploid conditions. There is no evidence of a deterioration of the germ plasm following allopolyploidy. When it first arises, as a single individual, a polyploid will be under the disadvantage of lacking the variability necessary for adaptive response to selection and will generally be cut off, by sterility barriers, from accession of variability from the parental species. On the other hand, allopolyploids will show vigour superior to that of the parents and once established and widely spread their plasticity will increase with the increase of their genetic variance. Polyploids are initially favoured by great environmental changes, such as those resulting from the Ice Age or from human activities.

Enough has, perhaps, been said to justify the opening sentences of this review. The book is a worthy swan song of the Cotton Research Station in Trinidad and a herald of future research by the Empire Cotton Growing Corporation on the genetics of cotton in Africa.

W. B. TURRILL

Ancient Plants and the World They Live in. By HENRY N. ANDREWS. $9\frac{1}{4} \times 6$ in., 279 pp., with 166 text-figs. New York: Comstock Publishing Co. 1947. Price \$4.50.

This is a book to read for pleasure or for general background, but it is not a text-book for any examination. It is written for the reader with no knowledge at all of palaeobotany, but sufficient knowledge of botany or else geology to have general interest, and it tells him what palaeobotany is about.

The method is to develop selected examples, mostly from the author's own experience; this leads to a preponderance of American illustrations which, to me at least makes the book all the more interesting. It begins and ends with the history of fossil botany and again and again we are told of the thrills of collecting (with pleasant but irrelevant detail). As a matter of fact the more familiar fossil families all appear, though in a very general way, thus the Calamites come in a chapter called 'Lingering relics of the Coal Age'. Other chapters deal with past climates, coal, and past fossil botanists. Certain points call for special praise. The text though frankly semi-popular is thoughtful and accurate; it is neither burdened with morphological detail, nor unnecessary names. The photographs are excellent and so are many new line drawings. A charming book.

T. M. HARRIS